

# Bothalia

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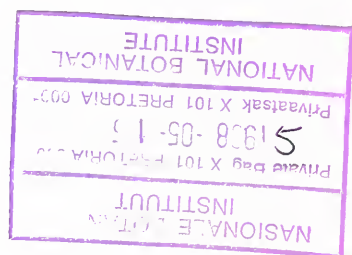
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## Studies in the liverwort genus *Fossombronia* (Metzgeriales) from southern Africa. 5. A new species from Northern and Western Cape

S.M. PEROLD\*

**Keywords:** *Fossombronia*, *F. cederbergensis*, Hepaticae, Metzgeriales, new species, southern Africa

### ABSTRACT

A new species of *Fossombronia*, *F. cederbergensis*, from the winter rainfall area of the Northern and Western Cape is described. It is characterized by 'ruched' leaves that are mostly wider than long, by tuberous stem apices that enable the plants to survive the hot, dry summers and by completely or incompletely reticulate spores.

### *Fossombronia cederbergensis* Perold, sp. nov.

Plantae prostratae, crebrae in coloniis. Folia imbricata, valde convoluta, forma irregulari, plerumque superne lobata, valde latiora quam longiora. Rhizoidea ad apicem ventralem caulis interdum hyalina, proximaliter purpurea. Caules apicem versus tuberosi. Dioicae. Plantae masculae rarissimae, parvulae; antheridia bracteis irregulariter formatis tecta. Plantae femineae maiores, pseudoperianthio campanulato, orificio undulato, subplicato vel partim reflexo. Sporae 37.5–50.0 µm diametro, ornamentis variis, superficie distali cum reticulo 11 vel 12 areolulis trans diametrum, sed saepe imperfecte reticulata; lamellis tenuibus, interdum subsinuatis, plerumque in nodis prominentibus; superficie proximali cum nota tri-radiata plerumque indistincta vel carenti, cum cristis brevibus irregularibus tenuibus vel pergrossis ramosis. Elateres 140–250 × 7.5–10.0 µm, extremitates versus decrescentes, ± 5 µm lati, bis vel ter spirales in centro, interdum leviter papillosi.

TYPE.—Northern Cape, 3219 (Wuppertal): 2 km south of Algeria Forest Station, at sandstone rock outcrop, on sandy soil, (–AC), *S.M. Perold* 2359 (PRE, holo.). Western Cape, 3218 (Clanwilliam): 21 km N of Citrusdal, on sandstone rock outcrops above Olifants River, Hex River Estates, (–BD), *S.M. Perold* 2380 (PRE, para.).

Plants in dense mats, fresh apical growth generally entirely green, except for some smaller young leaflets which are often stained throughout with various shades of purple, otherwise only leaf margins and scattered interior cells purple, proximal leaves frequently dying, becoming translucent and crumpled, sometimes only their basal remnants remaining in 2 oblique lines forming a row of disconnected 'Vs' dorsally along stem; shoots simple (Figure 2A) or once/twice furcate, branches sometimes developing from lateral buds; male plants very rare, rather small, up to 3.5 mm long, 0.75 mm high, ± 1.3 mm wide; female and sterile plants 9–13 mm long, 1.5 mm high, 1.75 mm wide, successive years' growth from apex of old stem, if branched, terminal segments

4–5 mm long, narrowly (Figure 2B) to moderately divergent. Stems prostrate, green, but sometimes dorsally pink or purple toward swollen apex, in cross section plano-convex, in male plants (Figure 1M) 280 µm (11 cell rows) high, 500 µm wide, becoming strongly arched and tapering toward base, 250 µm high, 400 µm wide; in female plants apically (Figure 1N) 370 µm (13 cell rows) high, 580 µm wide, basally (Figure 1O) 250 µm high, 320 µm wide. Rhizoids at apex of stem sometimes all hyaline, then becoming mixed with purple rhizoids, proximally all rhizoids purple, until next apex, giving rise to new growth, where some are again hyaline, 12.5–20.0 µm wide. Leaves in male plants overlapping, spreading, succubously inserted on stem, irregularly shaped, 'ruched' above (Figure 1A–E), 600–1000 × 650–850 µm, margins with ± 4 unicellular slime papillae, 20.0–22.5 × 15.0–17.5 µm, mostly along sides; in female plants leaves (Figure 1F–J) densely overlapping, very frilly (Figure 2C), shape irregular, generally shorter than wide, 575–700(–1625) × 650–1375(–1875) µm, often lobed above, lobes 250–320 × 280–450 µm, margins with up to 7 well-spaced papillae. Leaf cells not appreciably different in male and female plants, thin-walled, at upper margins subquadrate to rectangular across (Figure 1K), 25–45 × 27.5–45.0 µm, at lateral margins long-rectangular, 22.5–72.5 × 20.0–52.5 µm; upper laminal cells 5- or 6-sided, 35–70 × 37.5–42.5 µm; middle laminal cells 50–75 × 30–45 µm; basal cells 45.0–87.5 × 30–45 µm. Oil bodies in young leaves (Figure 1L) smooth, round, 7–19 per cell, variable in size, from minute to 2.5 µm diam.; chloroplasts oval or round, 2.5–5.0 µm diam.

Dioicous. Antheridia dorsal on stem, in a row, short-stalked, globose, ± 230 µm diam., mostly soon shed; bracts (Figure 1P–R) remaining, shape irregular, 575–700 × 650–1375 µm, with up to 3 finger-like processes and 2 or 3 marginal papillae, cells in interior 30.0–37.5 × 25.0–27.5 µm, basal cells 47.5–60.0 × 30.0–32.5 µm. Archegonia well spaced, in 1 or 2 irregular rows dorsally along stem (Figure 2D), 250–370 µm long, mostly obscured by strongly 'ruched' leaves. Pseudoperianth (Figures 1T, U; 2E, F) campanulate, proximal to stem apices, 1375–1625 µm long, projecting ± 875 µm above leaves, from narrow base widely flaring above, 1950–2575 µm wide across mouth, margin undulating to somewhat plicate or partly reflexed, occasionally with winged outgrowth at side; cells comparable in

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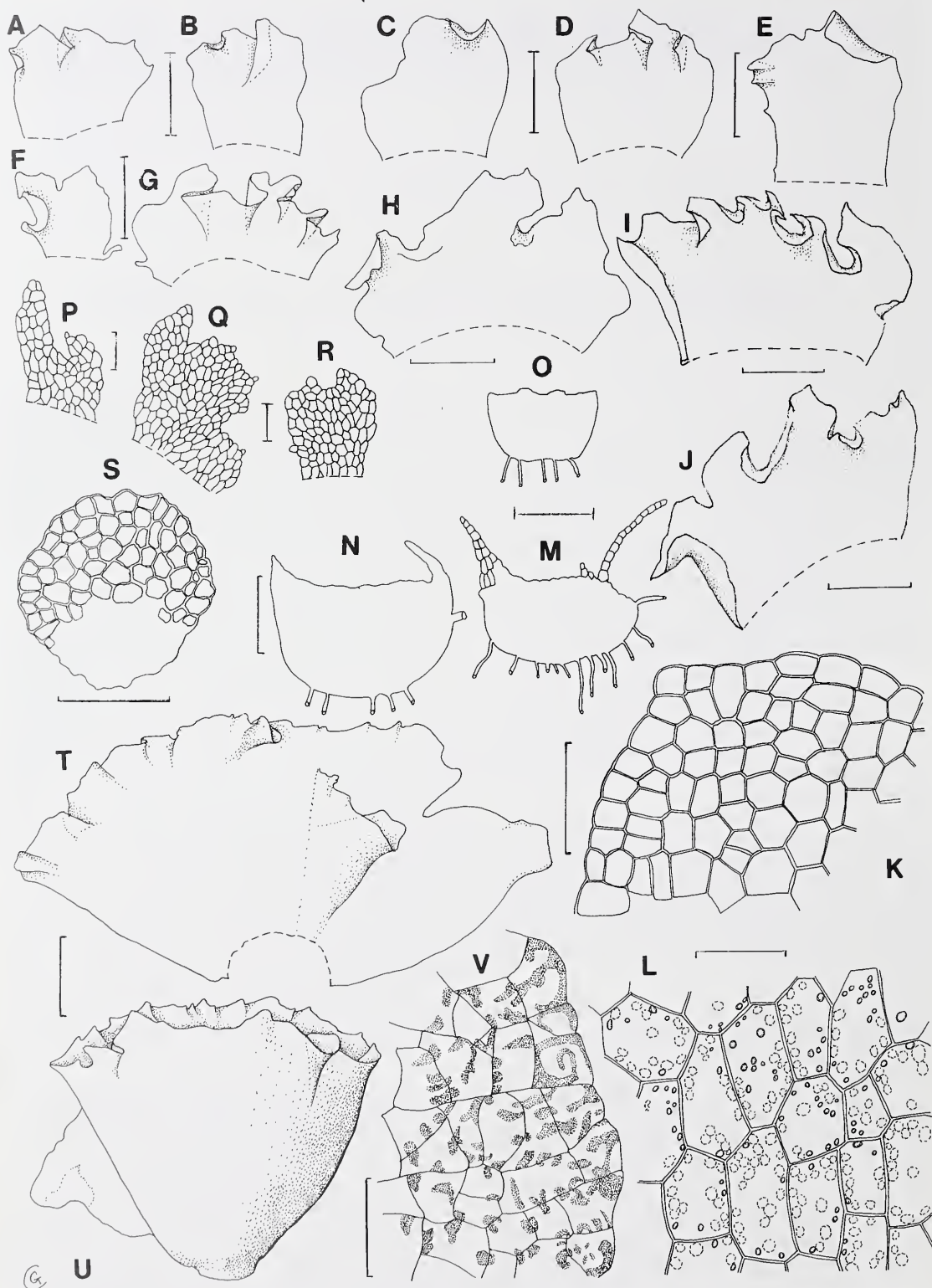


FIGURE 1.—*Fossombronia cederbergensis*. A–E, male leaves; F–J, female leaves; K, detail of upper leaf margin; L, median leaf cells with oil bodies (solid lines) and chloroplasts (dotted lines); M, cross section of apical part of male stem; N, cross section of apical part of female stem; O, cross section of basal part of female stem; P–R, bracts; S, cross section of seta; T, opened pseudoperianth; U, pseudoperianth from side; V, cells in capsule wall. A–E, M, O–R, *S.M. Perold* 2380; F, S–V, *S.M. Perold* 2359; G, *S.M. Perold* 2093; H–J, *S.M. Perold* et al. 3044; K–L, N, *Koekemoer* 1209. Scale bars: A–J, T, U, 500 µm; K, S, 100 µm; L, V, 50 µm; M–R, 250 µm. Artist: G. Condy.

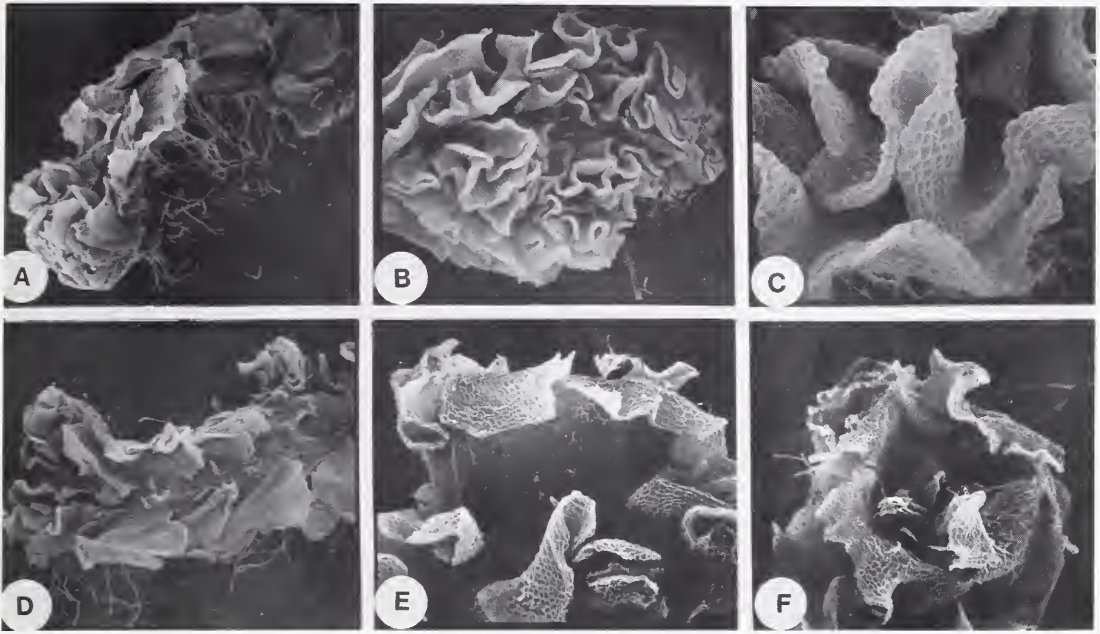


FIGURE 2.—*Fossombronina cederbergensis*. A, arched terminal segment from side, fresh young growth at apex; B, shoot with two narrowly divergent terminal segments; C, very frilly leaves in female plant; D, archegonia in 2 rows on stem, between leaves; E, F, pseudoperianth: E, from side; F, from above. A, D, *Koekemoer* 1209; B, C, E, F, *S.M. Perold* 2359. A,  $\times 18$ ; B,  $\times 17$ ; C,  $\times 83$ ; D,  $\times 16$ ; E,  $\times 31$ ; F,  $\times 22$ .

shape and size to those of leaves, except for rather longer, thin-walled basal cells,  $90.0\text{--}137.5 \times 37.5\text{--}47.5 \mu\text{m}$ . *Capsules* globose,  $\pm 700 \mu\text{m}$  diam., wall bistratose, cells of inner layer polygonal,  $25.0\text{--}42.5 \times 25\text{--}35 \mu\text{m}$ , each cell wall (Figure 1V) with 1–3 brown nodular and occasionally semi-annular thickenings. *Seta* 1.4–5.5 mm long,  $\pm 170 \mu\text{m}$  or 10 cell rows diam. (Figure 1S). *Spores* light to dark brown, hemispherical,  $(37.5\text{--})40.0\text{--}47.5$

$(\text{--}50.0) \mu\text{m}$  diam., including spines projecting at periphery (Figure 3D); distal face convex, ornamentation with a mesh of 11 or 12 small, up to  $5 \mu\text{m}$  wide, complete areolae (Figure 3C) across diam., but often incompletely reticulate (Figure 3A, B), lamellae thin, sometimes slightly sinuous, mostly raised at the nodes; proximal face with triradial mark (Figure 3E) generally indistinct or lacking, with short, irregular, fine to very coarse,

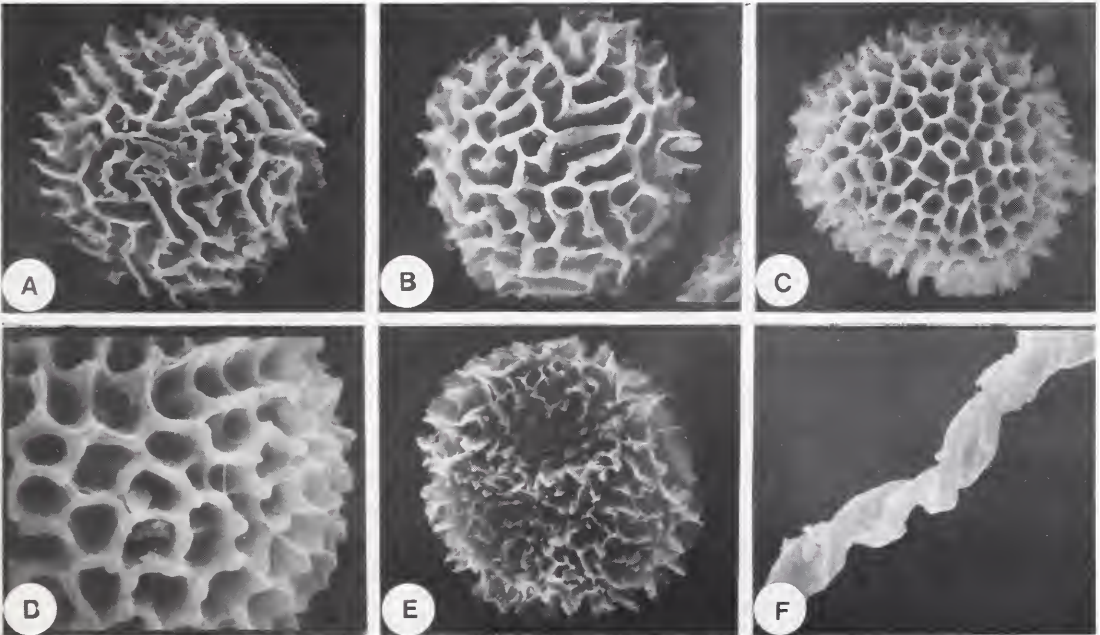


FIGURE 3.—*Fossombronina cederbergensis*. A–E, spores: A–C, distal face; D, detail of areolae on distal face; E, proximal face. F, elater. A, B, E, *S.M. Perold* 2359; C, D, F, *S.M. Perold* 2380. A,  $\times 771$ ; B,  $\times 990$ ; C,  $\times 693$ ; D,  $\times 1560$ ; E,  $\times 918$ ; F,  $\times 994$ .



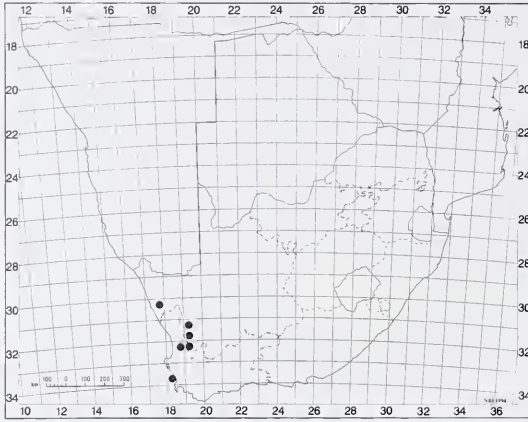


FIGURE 4.—The distribution of *F. cederbergensis* in Northern and Western Cape.

branched ridges, sometimes a few papillae present in between, around spore periphery  $\pm 25$  low spines projecting  $\pm 2.5$   $\mu\text{m}$ , occasionally more, (but difficult to count their number as only some seen 'end-on'), others with sides of lamellae showing. *Elaters* (Figure 3F) yellow-brown,  $140\text{--}250 \times 7.5\text{--}10.0$   $\mu\text{m}$ , tapering to tips,  $\pm 5$   $\mu\text{m}$  wide, bi- or sometimes trispiral in centre, occasionally finely papillose.

*Fossombronia cederbergensis* has been named for the Cederberg, where I first collected it. The species is known from several localities in the winter rainfall areas of Northern and Western Cape (Figure 4), with vegetation types, North-western Mountain Renosterveld and Mountain Fynbos (Low & Rebelo 1996). The plants often grow on slightly acid, rather sandy soil overlying sandstone outcrops, but sometimes on fine-grained, moisture retaining clay, at roadsides, dried seeps, stream banks or pond margins. Of the 12 specimens referred here, only three had spores, and they show rather wide variation in the ornamentation, from completely reticulate in *S.M. Perold* 2380 to incompletely reticulate in *S.M. Perold* 2359 and *Powrie* 182. The specimens that lack spores could be identified by vegetative characters. The swollen tuberos apices of the stems help the plants to survive the hot, dry summers. In some plants up to three seasons' growth could be detected. A sample of the specimen *Koekemoer* 1209, quickly resumed growth from the stem apices, nine months after collection, when kept wet in a closed plastic container for a few days.

The species can be distinguished by the 'ruched', lobed leaves, which are mostly wider than long, the tuberos stem apices, the completely or incompletely reticulate spores and by the occasional to frequent presence of some hyaline rhizoids. The tuberos apices of the stems bear some resemblance to those of *F. spinifolia* (Perold 1997b), which has markedly dentate leaves in the male plants, spores with 6 or 7 short irregular ridges, and which is only known from Genadendal.

Scott & Pike (1987) described many new species from Australia, one of which, *F. tessellata*, has spores similarly reticulate to those of *F. cederbergensis*, but they are a deep maroon, rather smaller at  $30\text{--}41$   $\mu\text{m}$  diam. and the

elaters are mostly shorter than those of the southern African species; its rhizoids are crimson throughout. *F. vermiculata* with purple and hyaline rhizoids mixed on the same stem was newly described by Scott & Pike (1984) and in the same publication they mention that in *F. scrobiculata* the rhizoids are hyaline on most plants but crimson on some, whereas in *F. punctata* they state that the rhizoids are '(?) always) hyaline, not crimson'. A species recently described from southern Africa, *F. straussiana* (Perold 1997a), always has hyaline or brownish rhizoids and in the European species, *F. husnotii*, the rhizoids are characteristically hyaline, although Scott & Pike (1988) claim that they are not all so. Whether having purple and hyaline rhizoids mixed on the same stem is really of taxonomic significance is not yet known. However, failure to observe the presence of hyaline or pale brown rhizoids 'may cause confusion' (Paton 1973). On some spore similarities, but rather poorly portrayed in their figures, Scott & Pike (1988: figs 13, 14) have placed *F. hamato-hirta* Steph. which has 'radicellis pallidis' (Stephani 1894) in synonymy under *F. wondraczekii* which has purple rhizoids. Perhaps this should be investigated further. The spore micrographs which I took of the type and only known specimen of *F. hamato-hirta*, *H.I. Gordon* 108 (G) from Ascension Island, bear quite a close resemblance to those of *F. straussiana* and as mentioned above, both have hyaline rhizoids. It is, however, not possible to make a definite decision on their synonymy with the available material of *F. hamato-hirta*.

#### SPECIMENS EXAMINED

Held at PRE, unless otherwise indicated.

*Koekemoer* 1209.

*S.M. Perold* 2093, 2197 (with *Riccia villosa* Steph.), 2323, 2359\* (holotype), 2364, 2380 (paratype)\*, 3336 (with *F. leucoxantha* Lehm.), 3339 (with *F. leucoxantha* Lehm.), 3355 (with *F. leucoxantha* Lehm.). *Perold*, *Koekemoer* & *Smook* 3044. *E. Powrie* 182\* (BOL).

\* sporulating specimens.

#### ACKNOWLEDGEMENTS

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# A taxonomic revision of *Maurocenia* (Celastraceae), a Western Cape monotypic endemic

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**Keywords:** Cassinoideae, Celastraceae, *Maurocenia* Mill., taxonomy, South Africa

## ABSTRACT

A taxonomic account is given of the monotypic genus *Maurocenia* Mill. *Maurocenia frangula* Mill. has a restricted range and is endemic to the Cape Peninsula and the West Coast National Park, Western Cape. *Maurocenia frangularia* (L.) Mill., the species name and author citation widely used in the past, is incorrect. It is characterized by, among others, pendulous ovules and gynodioecy, rare states in the Celastraceae. *Maurocenia* is apparently most closely related to the southern African genus *Lauridia* Eckl. & Zeyh.

## INTRODUCTION

The genus *Maurocenia* is fairly similar in many anatomical and morphological features to *Lauridia* Eckl. & Zeyh. (Archer & Van Wyk 1997). However, the pendulous ovules in *Maurocenia* set it apart from the other genera in the southern African Cassinoideae, which have erect ovules (Archer & Van Wyk 1996). The occurrence of pendulous ovules is relatively rare in the Celastraceae. Perhaps the genus is, on account of its ovule orientation, more closely related to the tropical American *Tetrasiphon* Urb. and *Gyminda* Sarg. (Loesener 1942; Brizicky 1964) than to the remaining southern African genera.

*Maurocenia frangula* was evidently not uncommon in cultivation in Europe in the 18th century, in view of the abundance of illustrations of the species. It was first introduced in 1690 to the Royal Botanic Gardens in London (Aiton 1811). In the pre-Linnaean period the species was described and illustrated by Plukenet (1691), Petiver (1702), Boerhaave (1710) and Dillenius (1732). The genus and phrase name of Dillenius (1732), *Maurocenia frangula sempervirens, folio rigido subrotundo* was taken up by Linnaeus (1737, 1743). However, in 1753 Linnaeus reduced *Maurocenia* to synonymy under *Cassine* L. The name *Maurocenia* was subsequently validly published when the genus was reinstated by Miller (1754), in an attempt to rectify what he thought was an error on Linnaeus's part. The epithet *frangula* was provided later (Miller 1768), being taken up from the phrase name. Willdenow (1798) first introduced the incorrect form of the epithet, *frangularia*, which is today in general use in herbaria and in most recent literature. The author citation in general use for the taxon, i.e. (L.) Mill. (Arnold & De Wet 1993), is also incorrect.

***Maurocenia* Mill.**, The gardener's dictionary [abridg. edn 4, 1754]: 859, facs. edn, Cramer (1969); Adans.: 303 (1763), as *Maurocena*; Sond.: 465 (1860); Kuntze: 147 & 149 (1891) p.p., excl. subg. *Triceros* Kuntze; Thonner: 331 (1915); Davison: 343 (1927); Loes.: 179 (1942); R.A.Dyer: 335 (1975). Type: *M. frangula* Mill.

*Maurocenia* Mill. subg. *Eumaurocenia* Kuntze: 149 (1891).

Small evergreen, gynodioecious shrub to spreading tree up to 8 m high, unarmed, glabrous, without elastic threads in leaves and bark; bark greyish with layers of powdery yellow pigment in exposed rhytidome, exfoliating in thin scales, surface cracked in grid-like pattern. *Branchlets* terete or slightly flattened, greyish brown to brown. *Leaves* opposite; lamina widely elliptic to circular, dark green above, grey-green below, (25–)35–60 (–85) × (20–)30–55 (–65) mm, base rounded to cuneate, apex rounded to retuse, margin entire, revolute, coriaceous and rigid; venation slightly raised above and more prominent below, reticulation inconspicuous, brochidodromous, midrib and petiole very conspicuous below owing to whitish green colour contrasting with grey-green of rest of lamina in dried leaves; petiole 2–3 mm long; stipules minute, ± 1 mm long, ± triangular, brownish black, marcescent. *Inflorescences* sessile, ± irregularly dichasial, axillary towards apices of branchlets, 4–10-flowered; bracts minute. *Flowers* often unisexual with staminodes (female), or bisexual, pentamerous, ± 2 mm diam.; pedicels 2–4 mm long. *Sepals* rudimentary, ± 0.3 mm long. *Petals* white, ovate, 1.3 × 1.0 mm, sessile, apex rounded, margin ± deflexed. *Stamens* ± erect; inserted below margin of disc; filaments of perfect flowers 3–4 mm long, well exerted above flowers; filaments of female flowers rudimentary (staminodes); anthers of perfect flowers 0.8 mm long, basifixed, introrse, dehiscent by longitudinal slits. *Disc* fleshy, entire, undulate. *Ovary* ± 1/3 immersed in and adnate to disc, 2(3)-locular with 2 pendulous collateral ovules per locule, brown, ± spheroid, post-chalazal vascular bundles not observed, fleshy endosperm present; embryo erect, with cotyledons fleshy, widely elliptic, base unequal (Figure 1).

***Maurocenia frangula* Mill.**, The gardener's dictionary edn 8.: no page number (1768); Willd.: 1493 (1798), in syn. as *frangularia*; Pers.: 327 (1805); Marloth: 153 (1925); Davison: 343 (1927); Loes.: 179

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FIGURE 1.—*Maurocenia frangula*. A, branch with female flowers,  $\times 0.7$ ; B, female flower,  $\times 7$ ; C, branch with perfect flowers,  $\times 0.7$ ; D, perfect flower,  $\times 7$ . Drawn from Marloth 5978 (PRE) by Anne Stadler.

(1942); Adamson: 567 (1950); Levyns: 190 (1966); Von Breitenbach: 640 (1965); Palmer & Pitman: 1324 (1973); Coates Palgrave: 515 (1977); Bond & Goldblatt: 224 (1984). Type: Dillenius, Hortus Eltham. t. 146, f. 147 (1732), lecto., here designated.

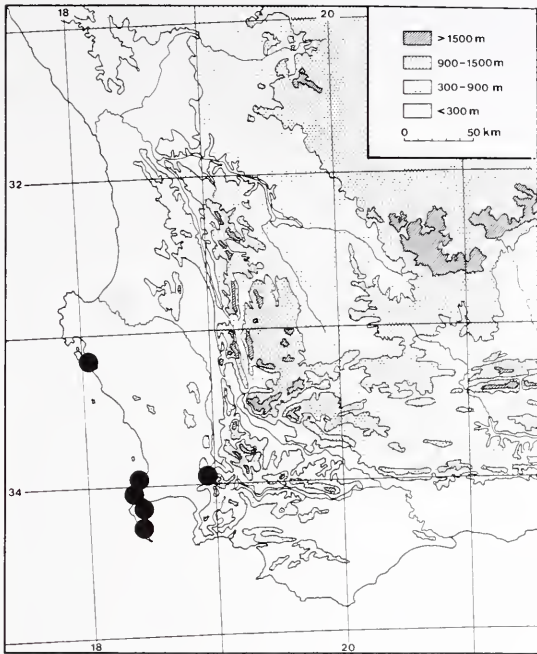
*Cassine maurocenia* L.: 269 (1753); 385 (1762); Willd.: 1493 (1798); Thunb.: 52 (1794); Thunb.: 225 (1818); Thunb.: 268 (1823); W.T.Aiton: 170 (1811); Roem. & Schult.: 466 (1819); Spreng.: 939 (1824); Eckl. & Zeyh.: 128 (1834/5); Hook.: t. 552 (1843); Sond.: 465 (1860); Hook.f.: 363 (1862); Szyzyl.: 33 (1888).

Icones: Pluk.: t. 158, f. 2 (1691); Petiver: t. 57, f. 4 (1702); Boerh.: 244 (1727); Dill.: t. 146, f. 147 (1732); Hook.: t. 552 (1843); Marloth: t. 51 (1925); Davison: t. 19 (1927); Von Breitenbach: 641 (1965).

*Maurocenia* is a monotypic genus of mountain kloofs and coastal bush on rocky sea shores in the Cape Peninsula and near Stellenbosch (Figure 2). *M. frangula*

is a gynodioecious shrub or tree, frequently encountered along the footpaths in the kloofs of Table Mountain. The wood is hard and has a fine grain, and has formerly been used in the manufacturing of musical instruments (Pappe 1854). Vernacular names are 'Hottentot's cherry' and 'Hottentot'skersie', referring to the fruit which is edible and was eaten by Khoikhoi (Hottentot). The genus name commemorates the Italian horticulturist, F. Mauroceni.

Although the species is described here as gynodioecious, it may well be dioecious. Further study is required to confirm the functional sexuality of the flowers. The long slender stamens would suggest an adaptation to wind pollination which is supported by the almost complete absence of sepals and deflexed petals. However, Marloth (1925) described the flowers as sweetly scented, visited by flies and bees.

FIGURE 2.—Known distribution of *Maurocenia frangula*.

### Specimens examined

WESTERN CAPE.—3318 (Cape Town): West Coast National Park, Postberg Peninsula, (–AA), *Van Wyk BSA 142* (PRU); 'Montis tabularis' [Table Mountain], (–CD), *Marloth 97* (PRE); Camps Bay, (–CD), *Marloth 5978* (PRE), *Maude s.n.* (BM), *Prior PRE-47256* (PRE, Z); Table Mountain, Grotto Ravine, (–CD), *Marloth 12044* (PRE); Stellenbosch, ridge behind Swartboskloof, adjoining Haelkop, (–DD), *Taylor 7301* (PRE). 3418 (Simonstown): Muizenberg, near False Bay, (–AB), *MacOwan 580* (BM, BOL, PRE, Z); slopes above Bakoven Bay, (–AB), *Marais 601* (BOL, PRE); Blackburn Kloof near Hout Bay, (–AB), *Marais 606* (PRE); Jagersfontein, (–AB), *Pole Evans 4349* (PRE); Hout Bay, (–AB), *Rehmann 1609* (Z), *Smuts 1154* (PRE); Boyes Drive, opp. St James, between Muizenberg and Kalkbaaiberg, (–AB), *Stauffer & Esterhuysen 5123* (PRE, Z); boulder near summit of Steenberg, (–AB), *Taylor 3296* (PRE); Cape of Good Hope Nature Reserve, Booiseskerm, (–AB), *Taylor 10531* (C, PRE); Cape Peninsula, West Coast opposite Antipolis shipwreck, (–AB), *Van Jaarsveld 3154* (PRE); Chapmans Peak, (–AB), *Van Jaarsveld 3171b* (PRE); Hout Bay, (–AB), *Wolley Dod 1045* (BM); Simonstown, Smitswinkelbaai, (–AD), *Schlechter 700* (Z); eastern side of Hangklip Peak, facing Blesberg, (–BD), *Rourke 1855* (NBG, PRE).

### Species excluded or insufficiently known

*M. americana* Mill. (1768)  
*M. arguta* (Lindl.) Kuntze: 149 (1891) = *Turpinia* sp. (Staphyleaceae)  
*M. cerasus* Mill. (1768)  
*M. cochinchinensis* (Lour.) Kuntze: 150 (1891) = *Turpinia* sp.  
*M. heterophylla* (Ruiz & Pav.) Kuntze: 150 (1891) = *Turpinia* sp.  
*M. insignis* (Kuntze) Kuntze: 149 (1891) = *Turpinia* sp.  
*M. occidentalis* (Sw.) Kuntze: 150 (1891) = *Turpinia* sp.  
*M. phylliraea* Mill. (1768)  
*M. pinnata* (Schiede ex Schldl.) Kuntze: 150 (1891) = *Turpinia* sp.  
*M. pomifera* (Roxb.) Kuntze: 147 & 149 (1891) = *Turpinia* sp.

*M. schinziana* Loes.: 194 (1894) = *Cassine parvifolia* Sond.  
*M. simplicifolia* (Gardner & Champ.) Kuntze: 149 (1891) = *Turpinia* sp.  
*M. sphaerocarpa* (Hassk.) Kuntze: 147 & 150 (1891) = *Turpinia* sp.  
*M. zollingeri* Kuntze: 147 (1891) = *Turpinia* sp.

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## FSA contributions 10: Trapaceae

B. VERDCOURT\*

Aquatic floating herbs. *Leaves* dimorphic: floating leaves alternate, in rosettes, only present at upper nodes, petiole spongy and more or less inflated about the middle; lamina rhombic to deltoid, the upper margins toothed, stipules small, scarious, divided to the base and thus apparently more than two per leaf; submerged leaves opposite, sessile, linear, entire, caducous. Adventitious roots developing from leaf scars of submerged leaves, containing chlorophyll, pinnatisect into many filiform segments; in those from upper nodes, segments shorter or absent. *Flowers* hermaphrodite, regular, 4-merous, solitary, from upper axils, pedunculate. *Sepals* 4. *Petals* 4, white. *Stamens* 4, perigynous. *Ovary* half-inferior, bilocular; ovules pendulous, 1 per locule; stigma capitate. *Fruit* a 1-seeded, top-shaped drupe; pericarp soon disappearing; endocarp hard, variously 2–4-horned; horns derived from persistent sepals; testa woody; cotyledons very unequal, 1 almost vestigial and not developing.

A single recent genus often included in the Onagraceae and seemingly closely related but with very distinct morphology. Miki (1959) has suggested derivation from Lythraceae and Corner (1976: 274) states that seed structure supports such an alliance and mentions that Maheshwari claims that embryological evidence denies close relationship with Onagraceae. *Hemitrapa* Miki, first described from the Miocene of Japan, is clearly distinct from *Trapa* and belongs with *Trapella* in Trapellaceae (~ Pedaliaceae). The adventitious roots have also been considered to be leaves but all the evidence (Couillault 1973) supports the other view.

### 5829000 TRAPA

**Trapa** L., Species plantarum 1: 120 (1753); L.: 56 (1754); Nakano: 440–458 (1913); A.Arber: 245 (1920); Gams: 884 (1925); Gams: 39–41, Karten 25–27 (1927); Steenis: 43 (1949); V.N.Vassil.: 638 (1949); Brenan: 1 (1953); Gams: 108–115, figs 1–6 (1958); Miki: 289–294 (1959); Nakano: 159–167 (1964); Sculthorpe: 328 (1967); C.D.K.Cook et al.: 537 (1974); Cronquist: 638 (1981); C.D.K.Cook: 217 (1990). Type species: *Trapa natans* L.

### Characters of the family.

About 70 species have been described, most of them from Russia and adjacent areas. Some 25–30 species are still maintained by Russian botanists but most others recognise only a few or even only one polymorphic species with numerous varieties. The latter appears to be the best course and is followed here, although Szafer

(1954) argues the contrary. Daniel *et al.* (1983: 596) would not even recognise varieties. There are many fossil species, the genus having occurred throughout the Tertiary and extending into the Upper Cretaceous. The generic name is a contraction of *calcitrappa* (Latin), a caltrop, a defensive weapon at one time used chiefly against cavalry and somewhat like the fruits of the plant.

**Trapa natans** L., Species plantarum 1: 120 (1753); Gams: 884, fig. 2263–2269, t. 190/1 (1925); Brenan: 1, fig. 1 (1953); Roessler: 1 (1966); Tutin: 303 (1968); D.F.Chamb.: 196 (1972); C.D.K.Cook et al.: fig. 262 (1974); Brenan: 346, fig. 85 (1978); Verdc.: 448 (1986). Type: S Europe, Italy, Mantua, L. Superiore, Fiori 471 (K, neo.!).

Annual with slender main axis 0.5–4.0 m long according to depth of water, unbranched or with 2–14 branches each ending in a floating rosette 150–500 mm wide. *Leaves*: blades often broader than long, 10–65 × 10–80 mm, glabrous above and beneath or hairy on nerves or densely hairy all over; petiole up to 210 mm long. *Sepals* lanceolate to narrowly triangular, 4–7 mm long. *Petals* oblanceolate to obovate, 8–16 mm long. *Fruit* up to ± 25 mm wide, very variably 2–4-horned.

Two varieties are distinguished in southern Africa:

Fruit 2-horned ... var. *bispinosa*

Fruit 4-horned ... var. *pumila*

5829000-1 var. **bispinosa** (Roxb.) Makino in Inuma, Somoku-Dzusetsu (?Iconography of plants in Japan) edn 3, 1: 137 (1907); Dubois: 399 (1954); Brenan: 3 (1953); R.Fern. & A.Fern.: 203 (1970); Brenan: 348 (1978). Type: India, Roxburgh (BM, lecto.!).

*T. bispinosa* Roxb. 3: 29, t. 234 (1815); Rech.f. 127: 1 (1978). *T. bicornis* Osbeck var. *bispinosa* (Roxb.) Nakano: 165 (1964).

*T. cochinchinensis* Lour., Flora cochinchinensis: 86 (1790). *T. bicornis* Osbeck var. *cochinchinensis* (Lour.) C.M.H.Gluck ex Steenis: 43 (1949); Backer & Bakh.f.: 265 (1963). Type: N Vietnam, Hanoi, Balansa 4526 (P, neo.).

*T. chinensis* Lour.: 86 (1790). Type: as for *T. bicornis* L.f., Plum.: t. 67 bottom (1693) (holo.!).

*T. austroafricana* V.N.Vassil.: 192, t. 12 (1965). Type: Zambia, Chingola, Fanshawe 2535 (K, holo.!, SRGH).

*T. congolensis* V.N.Vassil., op. cit. 184, figs 8, 9 (1965). Type: Zaire, Leopoldville, Couteaux 1014 (BR, holo.).

*T. insperata* V.N.Vassil., op. cit. 178, fig. 3 (1965). Type: Angola, R. Cubango, Gossweiler 2087 (P, holo.).

*Leaves* sometimes purplish beneath. *Fruit* ± 30–50 mm wide overall, 2-horned, horns arising from upper angles, erecto-patent to arcuate-ascending or almost horizontal, straight or somewhat curved, conical, or attenuate above, ± 10–18 mm long and ± 4–7 mm wide near

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FIGURE 1.—A–L, *Trapa natans* var. *bispinosa*: A, habit,  $\times 0.8$ ; B, part of leaf margin, lower surface,  $\times 3.8$ ; C, nodes showing stipules,  $\times 2.5$ ; D, flower,  $\times 2.5$ ; E, l.s. flower,  $\times 3.8$ ; F, two sepals,  $\times 3.8$ ; G, petal,  $\times 3.8$ ; H, anther, two views,  $\times 7.6$ ; I, ovary and disc,  $\times 7.6$ . J–L, fruit: J, endocarp,  $\times 1.2$ ; K, side view,  $\times 1.2$ ; L, apex of horn,  $\times 2.5$ . M–O, fruit of *T. natans* var. *pumila*: M, endocarp,  $\times 1.2$ ; N, side view,  $\times 1.2$ ; O, apex of horn,  $\times 2.5$ . A–D, Smith 2987; E–I, Biegel & Gibbs Russell 3714; J, K, Gibbs Russell 2786; L, Ellis 3073; M–O, Wager 37369.

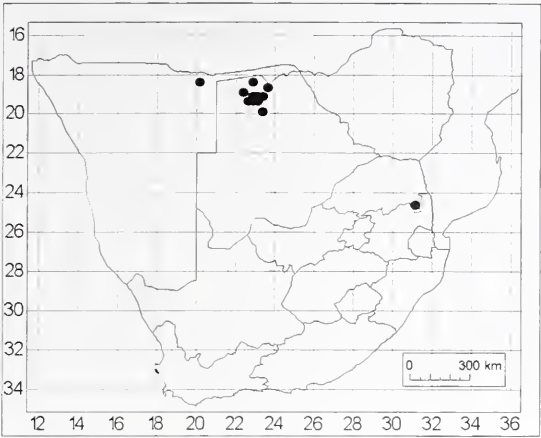


FIGURE 2.—Distribution of *Trapa natans* var. *bispinosa* in southern Africa.

base, sharp at point and usually reflexedly barbed for a little way below it; an additional inferior tubercle or short reflexed blunt horn may be present on each side and occasionally 2 further small projections above it. Figure 1A–L.

In NE Namibia along the Okavango River, N Botswana (Okavango Swamp) and Northern Province—formerly northeastern Transvaal (Figure 2). Also in W Africa, Zaïre, Sudan, Tanzania, Zambia, Zimbabwe, Malawi, Mozambique and Angola, throughout India, Indochina, China and Japan, also in Java. Rooted in soft mud in slowly flowing water, reedswamps, permanent pans etc.; 940–1 030 m.

Vouchers: Biegel & Russell 3714 (K; SRGH); De Winter & Marais 4473; 4765 (K, PRE); Dinter 7198 (K, PRE); Ellis 3073 (PRE).

The form with additional blunt horns (Van Cuong & Vidal loc. cit. 1973: t. 6/9) corresponds to var. *jinumai* Nakano.

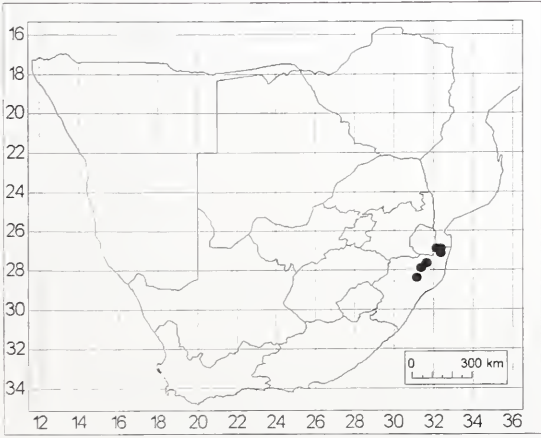


FIGURE 3.—Distribution of *Trapa natans* var. *pumila* in South Africa.

5829000-2 var. **pumila** Nakano ex Verdc. in Kew Bulletin 41: 448 (1986). Type: Vietnam, Hanoi, *Balansa* 4721 (P, holo.!, K, iso.!).

*T. natans* L. var. *incisa* Makino in Botanical Magazine, Tokyo 22: 172 (1908); Nakano: 454, t. 2/33–34 (1913) ‘grosse Formen’; *T. natans* L. var. *pumila* Nakano: 166 (1964); Van Cuong & J.E.Vidal: 46, t. 7/5–6 (1973) based on var. *incisa* ‘grosse Formen’ but no type cited, nom. invalid.

*Fruit* ± 40 mm wide overall, 4-horned, 2 fairly slender horns slightly ascending from upper angles 10–15 mm long and 2 strongly deflexed curved inferior horns mostly ± 10 mm long, all sharp and usually with reflexed barbs. Sometimes 2 additional short projections above inferior horns. Figure 1M–O.

In KwaZulu-Natal, Tongoland, Ingwavuma (Figure 3), also in Cameroon (*Saxer* 275), Japan, Indochina, Vietnam, India? Mainly in swamps and pans; 0–100 m.

Vouchers: Moll 1762 (PRE); Musil 46 (Univ. Nat.); Wager NH 37369 (NH, PRE).

Very likely *T. quadrispinosa* Roxb. (Type locality: Bangladesh, Sylhet) is this variant, but neither a specimen nor a drawing has been found; Vassiljev has chosen *Stewart* 3351½ from Kashmir as ‘lectotype’ although presumably neotype was meant. It is also what Glück was going to call *T. incisa* var. *quadricaudata* forma *laevigata* and forma *tuberculosa* in his proposed monograph. *T. natans* var. *africana* has much longer more slender ± equal spines.

The various forms of water chestnut are much cultivated, particularly in E Asia, and extensively used in Chinese cuisine. Nakano’s careful work over half a century has shown these are well-marked taxa but I have preferred to treat them as varieties. Unfortunately he did not follow normal taxonomic procedure of typification.

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# A revision of *Ledebouria* (Hyacinthaceae) in South Africa. 1. Two new species

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**Keywords:** Hyacinthaceae, *Ledebouria*, new species, South Africa, taxonomy

ABSTRACT

A revision of *Ledebouria* in South Africa has revealed a number of undescribed species. This paper deals with two new species, *Ledebouria atrobrunnea* S.Venter and *L. dolomiticola* S.Venter. Both species possess cylindrical bulbs, erect leaves (rare in *Ledebouria*) and prominent shoulders on the carpel apices. These synapomorphies are also seen in *L. viscosa* Jessop, and its allies.

INTRODUCTION

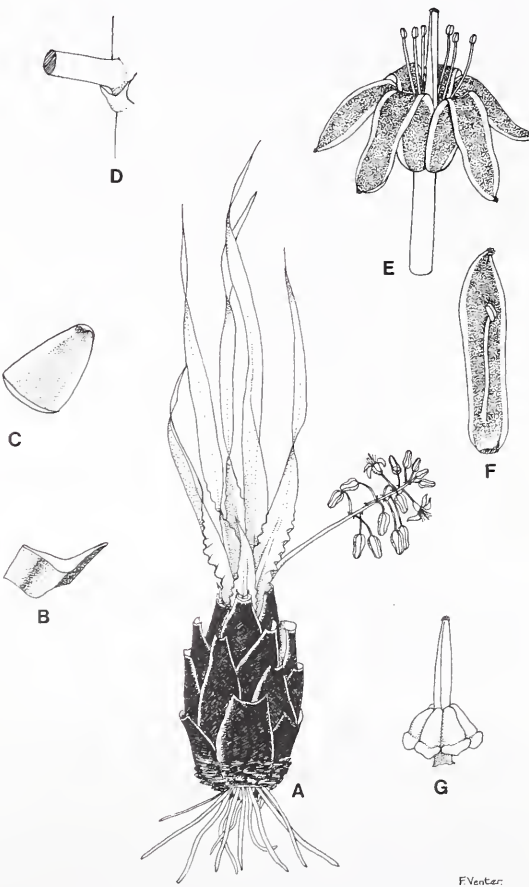
*Ledebouria* Roth includes some highly variable species and this has led to a proliferation of synonyms within the genus. Species plasticity, however, has also resulted in distinct taxa being overlooked in previous revisions (Jessop 1970). The species described in this account (*L. atrobrunnea* and *L. dolomiticola*) are based on characters which do not vary significantly between populations or in cultivated specimens. They form a natural group with *L. viscosa*, sharing cylindrical bulbs, erect leaves (rare in *Ledebouria*) and prominent shoulders on the carpel apices. All three species are exceedingly rare with very narrow distributions, features which make them particularly vulnerable to extinction.

1. *Ledebouria atrobrunnea* S.Venter, sp. nov. similis *L. viscosae*, sed foliis 4–6 (non solum 1–3), attenuatis (haud oblanceolatis usque spatulatis), non-viscosis tortisque et squamarum apicibus duris distincte differt.

TYPE.—North-West, 2527 (Rustenburg): Kroondal, Farm Zuurplaat 337, (–CD), Venter 13460 (PRE, holo.; NU, UNIN).

Plants solitary. *Bulb* hypogaeal, 30–60 × 20–30 mm, cylindrical, dead bulb scales purplish brown, very hard, attenuate, apices truncate, live bulb scales loose with threads when torn, bulb white and often purple-spotted. *Leaves* partly emerged at anthesis, 4–6, erect, spirally twisted, linear-lanceolate, 60–80 × 3–10 mm, with threads when torn, fleshy, dull glaucous, venation obscure; margin undulate in lower half, smooth above; base canaliculate, apex acute. *Inflorescences* 1–4, flaccid, lax, 30–60-flowered, longer than leaves; peduncle compressed at base, purple with darker spots, 25–60 mm long; rachis longitudinally ridged; raceme lax, oblong, 20–50 × 25–30 mm; bracts and bracteoles always present, slightly fleshy, 0.8–1.0 × 0.25–0.5 mm, linear to bifurcate, grey-white. *Pedicels* spreading, 6–7 mm long, speckled or pink. *Tepals* recurved, subequal, linear-

oblong, 4.0–5.0 × 1.5–2.0 mm, pink to purple, keel green; apex acute, slightly cucullate. *Stamens* erect, 3–4 mm long; filaments pink, base slightly flattened, epitepalous; anthers 0.75–1.0 mm long, violet. *Ovary* depressed, obtusely 6-lobed, 1.0–1.5 × 2.0–2.5 mm, lobes obtusely deltate, apical shoulders present, basal lobes present; stipe 0.25 × 0.25 mm; style 2.0–2.5 mm long, triangular in section, glabrous, purple. *Capsule*



F.Venter

FIGURE 1.—*Ledebouria atrobrunnea*, Venter 13460. A, habit, × 0.9; B, section through lamina, × 3; C, tepal apex, × 12; D, bract, × 12; E, flower, × 7; F, tepal with stamen, × 7; G, ovary lateral view, × 9. Drawing modified from Burrows (1993).

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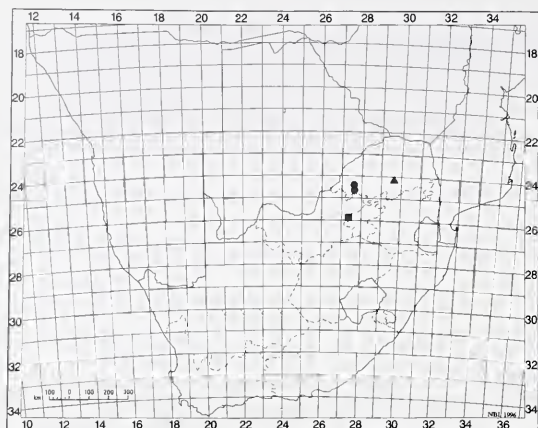


FIGURE 2.—Geographical distribution of *L. viscosa*, ○; *L. atrobrunnea*, ●.

clavate, base truncate. *Seed* 4–5 mm long, drop-shaped, strongly wrinkled, reddish brown. Figure 1.

This species is known only from Magaliesberg Quartzites of the Pretoria Group (SACS 1980) in the foothills of the Magaliesberg in the Kroondal area near Rustenburg (Figure 2). It occurs in shallow red-brown lithosols derived from coarse-grained recrystallised rock. Vegetation of the area is Bankenveld and consists of low closed deciduous *Protea caffra*–*Lanena discolor* Woodland (Acocks 1988).

The degree of leaf twisting and the prominence of bulb scales vary within *L. atrobrunnea*. Plants from exposed situations tend to have more prominent bulb scales and leaves more twisted than shaded individuals. The species flowers from September to late December.

*L. atrobrunnea* is related to *L. viscosa* Jessop which also has cylindrical bulbs and erect leaves. It is distinguished by its linear-lanceolate, non-viscid, twisted leaves and its hard purplish brown (hence the specific epithet) bulb scales. In *L. viscosa* the leaves are viscid, untwisted and oblanceolate to spatulate.

NORTH-WEST.—2527 (Rustenburg): Kroondal, Farm Zuurplaat 337, (–CD), *Venter* 13460 (NU, PRE, UNIN); *Venter* 13483 (PRE, UNIN).

2. *Ledebouria dolomiticola* S.Venter, sp. nov. similis *L. viscosae* et *L. atrobrunneae*, sed ab ambobus differt bulbis epigaeis. Praeterea ab illa foliis non-viscosis et ab hac bulbis squamis mortuis membranaceis (non duris) recedit.

TYPE.—Northern Province, 2429 (Zebediela): Strydpoort Mountain, Donkerkloof, Farm Rivierplaats 354, (–BA), *Venter* 13089a (PRE, holo.; NU, UNIN).

Bulbs epigeal, 40–100 × 15–30 mm, ellipsoid to cylindrical, in dense groups; dead bulb scales thinly membranous, brown, apices truncate, without threads when torn, live bulb scales tightly appressed, white inside, bulblets often present. *Leaves* fully developed at anthesis, 3–5, erect, lanceolate, 80–100 × 8–20 mm, without threads when torn, fleshy, glaucous, immaculate,

venation obscure; margin smooth; base canaliculate, apex acute. *Inflorescence* solitary, flaccid, lax, 30–40-flowered, longer than leaves; peduncle smooth, terete at base, green, 60–90 mm long; rachis smooth; raceme lax, cylindric, 40–60 × 20–30 mm; bracts with bracteoles, membranous, 1.50 × 0.25 mm, linear-lanceolate, grey to white. *Pedicels* spreading horizontally, 8–10 mm long, white to purple. *Tepals* recurved, subequal, oblong, 5 × 1.0–1.5 mm, pink to purple, keel green. *Stamens* erect, 3 mm long; filaments maroon, epipetalous; anthers 0.5 mm long, yellow. *Ovary* spheroidal, 1.5 × 2.5 mm, lobes narrowly transversely oblong; apex shoulders raised, basal lobes present; stipe 0.25–0.50 mm long; style 3 mm long, triangular in section, glabrous, purple above and white below. *Capsule* subglobose, base truncate. *Seed* 4 mm long, globose, strongly wrinkled, brown. Figure 3.

*L. dolomiticola* occurs in the Strydpoort Mountains near Pietersburg, Northern Province (Figure 2). Plants are limited to the Eccles Formation of the Chuniespoort Group (SACS 1980). The steep dolomitic slopes and cliffs on which *L. dolomiticola* grows experience high temperatures, especially during the summer months. Plants occur commonly in rock fissures and lithosols. Flowering occurs from January to April, as in *L. viscosa*.

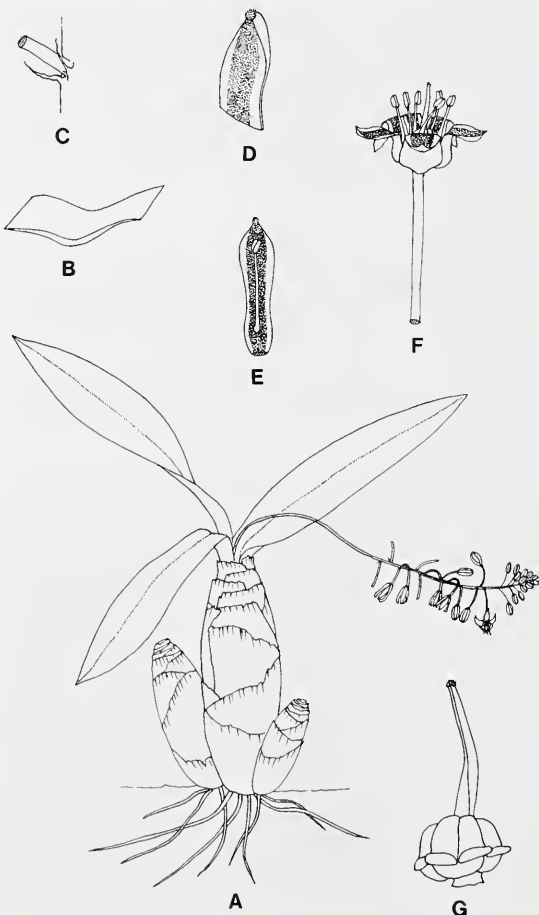


FIGURE 3.—*Ledebouria dolomiticola*, *Venter* 13089a. A, habit, × 0.3; B, section through lamina, × 1.3; C, bract with bracteole, × 4.4; D, tepal apex, × 6.3; E, tepal with stamen, × 3.8; F, flower, × 3.8; G, ovary, lateral view, × 6.3. Drawing modified from Burrows (1993).

*L. dolomiticola* is a close relative of *L. atrobrunnea* and *L. viscosa* which also possess cylindrical bulbs, erect leaves and prominent shoulders on the carpel apices. *L. dolomiticola* is distinguished from both by its epigeal bulbs and from *L. viscosa* by its non-viscous leaves and from *L. atrobrunnea* by its membranous dead bulb scales.

#### *Specimens of L. viscosa examined*

NORTHERN PROVINCE.—2427 (Thabazimbi): Kransberg, (–BC), Meeuse 10493 (PRE); Farm Waterval, Dyer & Ehrens 4201 (PRE); Farm Buffelshoek 446, (–DA), Venter 13455 (UNIN).

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## Revised key to *Ipomoea* (Convolvulaceae) in southern Africa

W.G. WELMAN\* and A.D.J. MEEUSE\*\*

**Keywords:** Convolvulaceae, *Ipomoea*, key, southern Africa

### ABSTRACT

A revised key to the 57 indigenous and naturalised species of *Ipomoea* L. in southern Africa is presented.

### INTRODUCTION

During the preparation of the Convolvulaceae for the *Flora of southern Africa* (FSA), Vol. 28, part 1, it became evident that the key to *Ipomoea* L. published by Meeuse (1957) in his revision of the South African Convolvulaceae had become outdated. As publication of this part of the FSA is not expected in the near future, it will be useful to publish a revised key now.

Meeuse (1957) listed 47 species of *Ipomoea* occurring naturally or naturalised in the southern African region. He also included *Stictocardia* Hallier f. (one species in southern Africa which can readily be confused with *Ipomoea*) and *Turbina sensu* Meeuse (seven species in southern Africa) in his key to *Ipomoea*. The list of *Ipomoea* in the region compiled by Welman (1993) contained 54 species, including *I. shupangensis* Baker and *I. urbaniana* (Dammer) Hallier f., both from tropical Africa; these are now excluded. The treatment of *Ipomoea* for FSA Vol. 28,1 will contain 57 species. Four are new records for the region namely *I. fanshawei* Verdc., *I. fulvicaulis* (Hochst. ex Choisy) Boiss. ex Hallier f. var. *fulvicaulis*, *I. ochracea* (Lindl.) G.Don, all from northern Botswana and *I. consimilis* Schulze-Menz from northern KwaZulu-Natal. The endemic *I. bisavium* A.Meeuse was described after the publication of Meeuse's revision: t. 1360 (1961).

In Meeuse & Welman (1996) some name changes are listed and explained. Six of the southern African species of *Turbina sensu* Meeuse are returned to *Ipomoea*, namely, *I. holubii* Baker [*T. holubii* (Baker) A.Meeuse], *I. oblongata* E.Mey. ex Choisy [*T. oblongata* (E.Mey. ex Choisy) A.Meeuse], *I. atherstonei* Baker], *I. oenotheroides* (L.f.) Raf. ex Hallier f. [*T. oenotheroides* (L.f.) A.Meeuse], *I. robertsiana* Rendle [*T. robertsiana*

(Rendle) A.Meeuse], *I. stenosphon* Hallier f. [*T. stenosphon* (Hallier f.) A.Meeuse], and *I. suffruticosa* Burch. [*T. suffruticosa* (Burch.) A.Meeuse]. The seventh species of *Turbina sensu* Meeuse in southern Africa is now *Paralepistemon shirensis* (Oliv.) Lejoly & Lisowski [*T. shirensis* (Oliv.) A.Meeuse] and is not included in this key. Two other name changes have taken place, namely, *I. dichroa* Choisy (*I. arachnosperma* Welw.), and *I. indica* (Burm.f.) Merr. (*I. congesta* R.Br.). Three varieties and one subspecies have been sunk, namely, *I. bathycolpos* Hallier f. (*I. bathycolpos* var. *sinuatodentata* Hallier f.), *I. magnusiana* Schinz [*I. magnusiana* var. *eenii* (Rendle) A.Meeuse], *I. obscura* (L.) Ker Gawl. [*I. obscura* var. *fragilis* (Choisy) A.Meeuse], and *I. bolusiana* Schinz (*I. bolusiana* subsp. *pinnatipartita* Verdc.). In Meeuse & Welman (1996) it is also mentioned that *I. carnea* Jacq. subsp. *fistulosa* (Mart. ex Choisy) D.Austin (*I. fistulosa* Mart. ex Choisy) should be excluded from the list of *Ipomoea* species in the region. However, it has recently become clear that this poisonous exotic plant often occurs as an escape from cultivation and it is therefore included in the revised key; see Welman (1997).

Some more exotic species have escaped from cultivation and are naturalised; these are also included in the key. Several other exotic species of *Ipomoea* are cultivated in especially the warmer parts of the region and may rarely occur as culture relics or garden escapes and are not included in the key, notably the following: *I. arborescens* (Kunth) G.Don (small tree with up to 50 mm long white flowers), *I. batatas* (L.) Lam. ('Sweet Potato'), *I. coccinea* L. (annual twiner with scarlet flowers), *I. horsfalliae* Hook. (perennial twiner with pink flowers), *I. intrapilosa* Rose (shrub or tree with up to 95 mm long white flowers), *I. quamoclit* L. (annual twiner with pinnate leaves and scarlet flowers), and *I. tricolor* Cav. (perennial twiner with predominantly blue flowers).

### KEY TO INDIGENOUS AND NATURALISED SPECIES

naturalised species indicated by \*

1a (1b: p. 23) Leaves simple, entire, shallowly lobed, emarginate or toothed, but not pinnately, palmately or pedately lobed nearly to base nor compound:

2a Flowers in pedunculate heads, surrounded by single large bicuspidate bract:

3a Sepals lanceolate, acute, glabrous or sparsely hairy, mainly at tips and along margins; corolla distinctly funnel-shaped, 30–50 mm long, limb 30–50 mm across; Northern Province . . . 27. *I. involucreata* P.Beauv.

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- 3b Sepals oblong-spathulate to oblong, obtuse, glabrous below tips inside; corolla tube slender, subcylindric,  $\pm 20$  mm long, limb spreading, 15–30 mm across; N Namibia, N Botswana, Mpumalanga . . . . . 28. *I. pileata* Roxb.
- 2b Flowers not in heads, or, if so, heads not subtended by one large and bicuspidate, boat-shaped bract:
- 4a (4b: p. 23) Corolla narrowly to widely funnel-shaped:
- 5a Leaves with minute black dots beneath; sepals  $\pm 8$  mm long, much-imbricate, subequal, glabrous, obovate, obtuse; KwaZulu-Natal . . . . . *Stictocardia laxiflora* (Baker) Hallier f.
- 5b Leaves without black dots (sometimes minutely pitted or pellucidly glandular):
- 6a Corolla small, under 18 mm long and/or its limb less than  $\pm 15$  mm across; flowers in fascicles, clusters or solitary, sometimes in pedunculate 1 to few-flowered cymes or heads:
- 7a Leaves when dry pellucidly glandular when seen in transmitted light, crisped along margin; sepals very unequal, outer ones ovate from cordate base, obtuse, markedly accrescent, crisped along margin; corolla 12–14 mm long, mauvish pink; capsule and seeds hairy; Namibia, Botswana, Northern Province, Northern Cape . . . . . 6. *I. hackeliana* (Schinz) Hallier f.
- 7b Leaves not pellucidly glandular:
- 8a Flowers in distinctly pedunculate, bracteate, dense heads; peduncle over 20 mm long; leaves entire, densely white tomentose beneath; corolla up to 15 mm long, pale yellow; erect to trailing annual; N Namibia, Botswana, Northern Province . . . . . 22. *I. chloroneura* Hallier f.
- 8b Flowers not in pedunculate bracteate heads; if fascicled or clustered, peduncles never longer than 20 mm:
- 9a Leaves hastate at base with entire or toothed basal auricles, very rarely all lanceolate; flowers solitary, rarely fasciculate; pedicels up to 12 mm; sepals linear, acuminate, hairy, 7–11 mm long; corolla pinkish mauve with darker centre, occasionally white; capsule hirsute; Northern Province, North-West, Gauteng, Mpumalanga . . . . . 5. *I. gracilisepala* Rendle
- 9b Leaves cordate, cuneate or truncate at base, never hastate:
- 10a Leaves usually 3-lobed, albotomentose beneath; flowers mauve-purple, in pedunculate dichasial 3–11-flowered cymes; N Namibia, N Botswana, Northern Province, Mpumalanga, Swaziland . . . . . 19. *I. dichroa* Choisy
- 10b Leaves entire, not albotomentose:
- 11a Leaves cuneate to truncate-rounded, rarely subcordate at base; flowers very small, sessile; corolla white, hardly longer than the usually bristly calyx; N Namibia, Botswana, Swaziland, N South Africa . . . . . 1. *I. coscinosperma* Hochst. ex Choisy
- 11b Leaves distinctly cordate at base:
- 12a Outer sepals cordate or auricled at base, attenuate into an acute apical portion; corolla about twice as long as calyx; peduncles distinct, over 10 mm long; inflorescences cymosely 1–3-flowered; Namibia, Botswana, Swaziland, N and E South Africa . . . . . 8. *I. sinensis* (Desr.) Choisy subsp. *blepharosepala* (Hochst. ex A.Rich.) Vcrdc. ex A.Meeuse
- 12b Outer sepals not as above; corolla slightly longer than calyx:
- 13a Leaf apex obtuse and minutely mucronate; petiole up to 20 mm long; inflorescences axillary, 1–3-flowered, subsessile; Caprivi, N Botswana . . . . . 3. *I. leucanthemum* (Klotzsch) Hallier f.
- 13b Leaf apex acute, subacute or acuminate; petioles up to 80 mm long:
- 14a Flowers usually in clusters; sepals very hairy, ovate-lanceolate with linear-acuminate, spreading tips; capsule hairy; seeds glabrous; Botswana, Northern Province, Gauteng, Mpumalanga . . . . . 2. *I. eriocarpa* R.Br.
- 14b Flowers solitary or in 2–5-flowered cymes; sepals obtuse or subacute, ciliate or nearly glabrous; capsule glabrous or with a few bristly hairs; seeds densely pubescent; N Namibia, N Botswana, Northern Province, Mpumalanga, Swaziland, KwaZulu-Natal . . . . . 4. *I. plebeia* R.Br. subsp. *africana* A.Meeuse
- 6b Corolla larger to very large, over 18 mm long; flowers usually pedunculate:
- 15a Leaves bilobed at apex, coriaceous or subcoriaceous, whole plant glabrous; stems stout, trailing; growing only on sandy beaches; KwaZulu-Natal, Western and Eastern Cape . . . . . 37. *I. pes-caprae* (L.) R.Br. subsp. *brasiliensis* (L.) Ooststr.
- 15b Leaves not bilobed (sometimes emarginate) at apex, or not found on sandy beaches:
- 16a Leaves cordate-ovate in outline, shallowly 3-lobed, or entire, cordate, cordate-ovate or cordate-deltoid, covered with thin white cobwebby tomentum beneath (occasionally reduced to a few scattered floccose patches); flowers mauve or magenta; bracteoles and sepals lanceolate or linear-lanceolate, acute to acuminate-aristate:
- 17a Flowers in dense globose pedunculate heads; corolla 20–40 mm long; Northern Province, Mpumalanga, KwaZulu-Natal, Eastern Cape . . . . . 20. *I. wightii* (Wall.) Choisy
- 17b Flowers in few- to many-flowered dichasia or cymes, sometimes solitary:
- 18a Corolla 18–25 mm long; N Namibia, N Botswana, Northern Province, Mpumalanga, Swaziland . . . . . 19. *I. dichroa* Choisy
- 18b Corolla 40–60 mm long; Swaziland, KwaZulu-Natal, Eastern Cape . . . . . 21. *I. ficifolia* Lindl.
- 16b Leaves either not with white cobwebby tomentum or bracts and sepals different (and if so, corolla white or pale mauve):

- 19a Leaves linear or lanceolate with narrow or sometimes somewhat rounded base, entire or sometimes toothed, repand, lobed or  $\pm$  emarginate; plants erect to prostrate, often suffruticose:  
20a Vegetative parts pubescent; calyx tomentose or pubescent:  
21a Vegetative parts (at least on younger shoots) and calyx usually covered with an adpressed, short and silvery pubescence:  
22a Erect, much-branched shrub; leaves linear or oblanceolate, sessile or subsessile, narrowed at base; flowers solitary on very short peduncles; Namibia, North-West, Free State, KwaZulu-Natal, Northern and Eastern Cape; endemic . . . . . 13. *I. oenotheroides* (L.f.) Raf. ex Hallier f.  
22b Prostrate or suberect perennial; leaves usually distinctly petiolate, rounded or subcordate at base; flowers solitary or 2 together; peduncles 10–50 mm long; Namibia, North-West, Northern Cape; endemic . . . . . 15. *I. suffruticosa* Burch.  
21b Vegetative parts usually not with adpressed short and silvery tomentum:  
23a Sepals unequal; plant hairy; Namibia, Botswana, N and E South Africa, Swaziland, Lesotho . . . . . 9. *I. crassipes* Hook.  
23b Sepals equal or subequal:  
24a Sepals acuminate to aristate; leaves usually long-attenuate at base and well over 50 mm long, usually also some toothed or pinnatisect, hairy or glabrous above; pubescence soft, white; N Namibia, Botswana, Northern Province, North-West, Gauteng . . . . . 7. *I. oenotherae* (Vatke) Hallier f.  
24b Sepals acute or acuminate; leaves not as above:  
25a Leaves under 50 mm long, entire, on a short petiole or subsessile, glabrous above; pubescence soft, white; Northern Province, Mpumalanga; endemic . . . . . 14. *I. robertsiana* Rendle  
25b Leaves usually over 50 mm long, entire, hairy above and below; pubescence usually stiff, adpressed on leaves, yellowish or brownish; Namibia, Botswana, central and E southern Africa . . . . . 24. *I. oblongata* E.Mey. ex Choisy  
20b Vegetative parts (at least the leaves) glabrous; stems occasionally minutely scabrid-hirsutulous:  
26a Corolla white, 20–35 mm long; plant stemless or with short stem; leaves entire or with few teeth; mainly E southern Africa, not Swaziland; endemic . . . . . 38. *I. simplex* Thunb.  
26b Corolla magenta or pale mauve with darker centre, over 25 mm long:  
27a Leaves usually over 5 mm wide; corolla pale mauve with darker centre; stems usually stout, sometimes minutely scabrous or hirsutulous; Namibia, Botswana . . . . . 39. *I. welwitschii* Vatke ex Hallier f.  
27b Leaves usually less than 5 mm wide; corolla magenta; stems often slender, glabrous; mainly N southern Africa . . . . . 40. *I. bolusiana* Schinz  
19b Leaves broader, not linear or lanceolate or, if narrow, broadly truncate, hastate, sagittate or cordate at base:  
28a (28b: p. 23) Annual or perennial plants, herbaceous, prostrate or climbing, sometimes suffruticose and suberect, but if so, under 500 mm high, never tall and woody:  
29a Stems thick, trailing, hollow or spongy, rooting at nodes; in moist, marshy, inundated localities or even completely aquatic, floating; N Namibia, N Botswana, N KwaZulu-Natal . . . . . 36. *I. aquatica* Forssk.  
29b Stems not thick, hollow or spongy or rooting at nodes and plant not usually found in very moist localities:  
30a (30b: p. 22) Leaves distinctly cordate or sagittate at base:  
31a Corolla either yellow and concolorous, or white or yellow with a purple or brown centre; sepals subequal, 4–8 mm long:  
32a Corolla up to 25 mm long; N and E southern Africa . . . . . 29. *I. obscura* (L.) Ker Gawl. var. *obscura*  
32b Corolla 27 mm long or longer; Botswana . . . . . 30. *I. ochracea* (Lindl.) G.Don var. *ochracea*  
31b Corolla pink, mauve, magenta, purple to blue or pure white, if white or yellowish with purple or magenta centre; sepals very unequal and over 8 mm long:  
33a Sepals entirely glabrous:  
34a Petiole short, under 15 mm long; leaves usually under 50 mm long; plant usually hairy in some part other than calyx; corolla with small tufts of hairs protruding from mid-petaline areas; Northern Province, North-West, Gauteng, Mpumalanga . . . . . 31. *I. transvaalensis* A.Meeuse  
34b Petioles 15–200 mm long:  
35a Leaves cordate-elliptic or rounded to subreniform, obtuse with minute cusps, basal sinus narrow and deep; sepals 12–20 mm long; corolla 35–70 mm long; mainly N South Africa; endemic . . . . . 32. *I. bathycolpos* Hallier f.  
35b Leaves cordate-deltoid or cordate-ovate, usually suddenly acuminate from broad, usually irregularly and coarsely few-toothed base into an entire apex, basal sinus broad; sepals 5–9 mm long; corolla 20–35 mm long; Botswana, Swaziland, N South Africa . . . . . 33. *I. papilio* Hallier f.  
33b Sepals thinly to densely hairy or tomentose:



- 36a Sepals long-attenuate or linear-acuminate at apex, 14–25 mm long; twining herbaceous plants with retrorse hairs on stems and petioles; leaves often 3-lobed:
- 37a Outer sepals lanceolate at base with long and linear acumens, patently hirsute in basal portion, 17–25 mm long; cultivated and naturalised; N Namibia . . . . . 16.\* *I. nil* (L.) Roth
- 37b Outer sepals lanceolate to ovate-lanceolate, gradually attenuate towards apex, with adpressed pubescence, 14–22 mm long; cultivated and naturalised; Gauteng, Mpumalanga, Swaziland, KwaZulu-Natal, Eastern and Western Cape . . . . . 18.\* *I. indica* (Burm.f.) Merr.
- 36b Sepals acute, obtuse or mucronate but not with long and narrow acumens, if sepals long-acuminate, plant not twining and without retrorse hairs on stems and petioles:
- 38a Calyx with bristly patent hairs in basal portion; glabrous towards apex; twining annual with retrorse hairs on stems and petioles; cultivated and naturalised; N and E South Africa . . . . . 17.\* *I. purpurea* (L.) Roth
- 38b Calyx not with bristly patent hairs in basal portion and glabrous towards apex:
- 39a Twining plant, growing in moist places (river banks, marshes, pools), often among reeds, sedges etc.; N Namibia, N Botswana . . . . . 48. *I. rubens* Choisy
- 39b Prostrate to suberect plants, or erect shrubs:
- 40a Plants prostrate to suffrutescent, if suberect never more than 500 mm high; corolla usually magenta:
- 41a Bracts usually close to calyx, never foliaceous; sepals subequal:
- 42a Bracts ovate, acuminate; Caprivi, N Botswana . . . . . 12. *I. fulvicaulis* (Hochst. ex Choisy) Boiss. ex Hallier f. var. *fulvicaulis*
- 42b Bracts linear or lanceolate, rarely broader; Namibia, Botswana, central and E southern Africa . . . . . 24. *I. oblongata* E.Mey. ex Choisy
- 41b Bracts usually distant from calyx, often foliaceous; sepals very unequal, outer ones ovate-acuminate, inner ones linear; Namibia, Botswana, N and E South Africa, Swaziland, Lesotho . . . . . 9. *I. crassipes* Hook.
- 40b Plant shrubby, erect; stems woody; sepals very broad, unequal; corolla pale mauve with magenta centre; Namibia, Botswana, Northern Province, Mpumalanga . . . . . 52. *I. holubii* Baker
- 30b (30a: p. 21) Leaves not distinctly cordate or sagittate at base:
- 43a Sepals entirely glabrous, sometimes rugose or muriculate:
- 44a Sepals 5–12 mm long:
- 45a Sepals 5–9 mm long; corolla magenta; leaves acuminate from broad base, coarsely toothed in lower half; Botswana, Swaziland, N South Africa . . . . . 33. *I. papilio* Hallier f.
- 45b Sepals 8–12 mm long; corolla pale mauve with darker centre; leaves linear-oblong to elliptic, entire, emarginate or 3-lobed, not broad or toothed at base; Namibia, Botswana . . . . . 39. *I. welwitschii* Vathek ex Hallier f.
- 44b Sepals 12–25 mm long:
- 46a Leaves rhomboid-lanceolate in outline, margin entire to lobed; sepals 15–18 mm long; corolla pale purple or mauve; Botswana . . . . . 46. *I. faushawei* Verdc.
- 46b Leaves oblong, elliptic, ovate to linear-oblong, entire; sepals 12–25 mm long; corolla magenta; Namibia, Botswana, central and E southern Africa . . . . . 24. *I. oblongata* E.Mey. ex Choisy
- 43b Sepals more or less hairy to tomentose:
- 47a Plant shrubby, erect, over 500 mm high; sepals very broad, suborbicular, rounded, unequal, inner ones larger; Namibia, Botswana, Northern Province, Mpumalanga . . . . . 52. *I. holubii* Baker
- 47b Plant prostrate; sometimes suffrutescent, suberect, but if so, under 500 mm high and sepals not very broad and rounded:
- 48a (48b: p. 23) Flowers in pedunculate, few to many-flowered heads (heads occasionally binate):
- 49a Bractcoles and sepals linear, narrow, bristly with long yellowish hairs; Mpumalanga, Swaziland, E Free State, KwaZulu-Natal, Eastern Cape; endemic . . . . . 10. *I. pellita* Hallier f.
- 49b Bractcoles and sepals lanceolate to ovate:
- 50a Leaves lanceolate or ovate-lanceolate from broad base to long-triangular, gradually narrowed towards apex; corolla bright magenta, 30–50 mm long; Botswana, Northern Province, North-West, Gauteng, Mpumalanga, Free State . . . . . 23. *I. omaneyi* Rendle
- 50b Leaves usually oblong to ovate and not often gradually tapering to apex from broad base:
- 51a Corolla magenta, 50 mm or longer; Namibia, Botswana, central and E southern Africa . . . . . 24. *I. oblongata* E.Mey. ex Choisy
- 51b Corolla mauve or purple, 25–50 mm long; Caprivi, N Botswana . . . . . 12. *I. fulvicaulis* (Hochst. ex Choisy) Boiss. ex Hallier f. var. *fulvicaulis*

48b (48a: p. 22) Flowers solitary or 2 or 3 together, or not in heads but in cymes:

52a Sepals very unequal; outer ones ovate or lanceolate from broad base, inner ones linear; bracts usually distant from the calyx and often foliaceous; Namibia, Botswana, N and E South Africa, Swaziland, Lesotho . . . . . 9. *I. crassipes* Hook.

52b Sepals equal or not so distinctly unequal:

53a Leaves up to 45 mm long, broad at base, often subcordate; bracteoles very minute; calyx 7–8 mm long; corolla bright magenta-rose, 20–40 mm long with small tufts of hairs protruding from midpetaline areas (especially conspicuous in older buds); Northern Province, North-West, Gauteng, Mpumalanga . . . . . 31. *I. transvaalensis* A.Meeuse

53b Leaves, bracts, sepals or corolla longer or corolla, if hairy on midpetaline areas, without protruding hair tufts:

54a Bracteoles distant from, more rarely contiguous to calyx; leaves quite glabrous above; corolla thinly hairy to glabrous on midpetaline areas; Northern Province, Mpumalanga; endemic . . . . . 14. *I. robertsiana* Rendle

54b Bracteoles contiguous to calyx; leaves usually hairy on both sides; corolla silky on midpetaline areas; Eastern Cape; endemic . . . . . 34. *I. crispa* (Thunb.) Hallier f.

28b (28a: p. 21) Tall perennial woody climbers or shrubs over 500 mm high:

55a Calyx glabrous:

56a Sepals orbicular to oblong, obtuse; leaves usually lobed, rarely entire; KwaZulu-Natal . . . . . 49. *I. mauritiana* Jacq.

56b Sepals ovate, cuspidate to acute; leaves entire, usually appearing after flowers; Caprivi, N Botswana, Northern Province . . . . . 50. *I. shirambensis* Baker

55b Calyx at least partly hairy, pubescent or tomentose:

57a Sepals broadly elliptic or obovate to orbicular, obtuse, 5–16 mm long, two inner ones larger than outer ones; shrubs; leaves not longer than 250 mm:

58a Leaves cordate-ovate, usually under 50 mm long; erect shrub with ultimate twigs sometimes flexuous or twining; corolla 40–50 mm long; Namibia, Botswana, Northern Province, Mpumalanga . . . . . 52. *I. holubii* Baker

58b Leaves ovate to lanceolate, 100–250 mm long; erect to scrambling shrubs to 3 m high; sepals suborbicular, 5–6 mm long; corolla 50–90 mm long; cultivated and seminaturalised; Northern Province, Mpumalanga, Swaziland, KwaZulu-Natal . . . . . 54. \**I. carnea* Jacq. subsp. *fistulosa* (Mart. ex Choisy) D.F.Austin

57b Sepals not as above; plants climbing; leaves mostly much larger:

59a Two outer sepals cordate-triangular, 14 mm long; young parts and peduncles not densely hairy; Northern Province; endemic . . . . . 11. *I. bisavium* A.Meeuse

59b Two outer sepals not as above; young parts densely hairy, as are peduncles:

60a Young parts densely white-tomentose:

61a Young leaves with very conspicuous reticulate, somewhat floccose tomentum on main veins below, older ones glabrescent; calyx at first tomentose, at least near base; corolla white, 60–90 mm long; Northern Province, Mpumalanga, Swaziland, KwaZulu-Natal . . . . . 55. *I. albivenia* (Lindl.) Sweet

61b Young leaves with complete tomentum below, tomentum usually persistent; calyx tomentose; corolla white, rose-purple or mauve with darker throat, 60–100 mm long; Namibia, N Botswana . . . . . 56. *I. verbascoidea* Choisy

60b Young parts densely yellow-villous; sepals linear-lanceolate; N KwaZulu-Natal . . . . . 57. *I. consimilis* Schulze-Menz

4b (4a: p. 20) Corolla salver-shaped, white or white with inside of tube purple or magenta:

62a Plant herbaceous and twining:

63a Corolla tube up to  $\pm$  40 mm long; leaves ovate to lanceolate, entire, cuneate to rounded at base; sepals not awned; N Namibia, Botswana, Northern Province, Mpumalanga, Swaziland . . . . . 35. *I. lapathifolia* Hallier f.

63b Corolla tube at least 70 mm long; leaves cordate at base, entire or 3-lobed; sepals awned; cultivated and naturalised; Mpumalanga, KwaZulu-Natal, Eastern Cape . . . . . 47. \**I. alba* L.

62b Plant not herbaceous and twining:

64a Plant shrubby, erect; calyx densely silky outside; Namibia, Botswana, Northern Province, Gauteng, Mpumalanga . . . . . 51. *I. adenioides* Schinz

64b Plant woody and climbing; calyx glabrous; sepals obtuse; Northern Province . . . . . 53. *I. stenosphon* Hallier f.

1b (1a: p. 19) Leaves deeply lobed (nearly to base), dissected or compound:

65a Leaves albotomentose below with prominent veins, palmately 3–5- or almost 7-lobed; Namibia, Botswana, Swaziland, mainly central and N South Africa . . . . . 25. *I. magnusiana* Schinz

65b Leaves glabrous or sometimes hairy but not albotomentose:

66a Flowers in dense pedunculate and bracteate heads; leaves hairy; N Namibia, Caprivi, N Botswana, Mpumalanga . . . . . 26. *I. pes-tigridis* L. var. *pes-tigridis*

- 66b Flowers solitary, fascicled or in cymes:
- 67a Corolla small, white tinged with mauve, 10–15 mm long; leaves palmately 5–7-fid with dentate or serrate to pinnatisect segments; Namibia, N Botswana, mainly N South Africa . . . . . 41. *I. coptica* (L.) Roth ex Roem. & Schult.
- 67b Corolla usually larger, rarely white; leaf segments not dentate or serrate, entire or basal ones with lateral lobe:
- 68a Large glabrous perennial climber; leaves palmately 3–9-lobed, 60–150 × 60–200 mm, not pseudostipulate; KwaZulu-Natal . . . . . 49. *I. mauritiana* Jacq.
- 68b Annuals or prostrate perennials, leaves much smaller, usually under 80 mm across and often pseudostipulate by small leaves of developing or suppressed axillary shoots:
- 69a Leaves usually pseudostipulate, distinctly palmately or pedately 5–9-fid, quite glabrous; climbing or occasionally prostrate annuals:
- 70a Calyx 8–10 mm long, outer sepals saccate at base; corolla yellow with mauve tube, 30–60 mm long and across; leaves usually biternately pedate often with 9 segments; N Namibia, N Botswana . . . . . 42. *I. tuberculata* Ker Gawl.
- 70b Calyx up to ± 7 mm long, outer sepals not saccate; corolla mauve, purple or white; leaves palmately partite with usually 5 segments:
- 71a Corolla 30–60 × 40–60 mm, mauve, rarely white; NE southern Africa . . . . . 43. *I. cairica* (L.) Sweet
- 71b Corolla up to ± 25 mm long:
- 72a Peduncles very slender, filiform; corolla often under 16 mm long, purplish mauve; N Namibia, Northern Province, Mpumalanga . . . . . 45. *I. tenuipes* Verdc.
- 72b Peduncles rather stout, not filiform; corolla 15–25 mm long, purplish mauve or white; Namibia, Botswana, Northern Province, Gauteng, Mpumalanga, Swaziland . . . . . 44. *I. hochstetteri* House
- 69b Leaves not pseudostipulate, pinnately dissected, tridentate or palmately compound; stems prostrate or rarely suberect from perennial tuberous rootstock; corolla usually over 30 mm long:
- 73a Young parts and sepals with soft white hairs; sepals very acute; basal leaves, if present, linear, cauline leaves tridentate to pinnatisect or all leaves pinnatisect; flowers solitary on short peduncles, deep pink to magenta; N Namibia, Botswana, Northern Province, North-West, Gauteng . . . . . 7. *I. oenotherae* (Vatke) Hallier f.
- 73b Sepals glabrous:
- 74a Leaves palmately 3–9-fid with linear segments under 5 mm wide (often very narrow); corolla magenta; stems often rather slender, glabrous; mainly N southern Africa . . . . . 40. *I. bolusiana* Schinz
- 74b Leaves trisect with linear, lanceolate or oblong segments usually over 5 mm wide; corolla pale mauve with magenta centre 30–80 mm long; stems usually stout; Namibia, Botswana . . . . . 39. *I. welwitschii* Vatke ex Hallier f.

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# Taxonomic notes on the genus *Khadia* (Mesembryanthemaceae/Aizoaceae)

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## ABSTRACT

The taxonomic status of the five species that comprise *Khadia* N.E.Br. is clarified on the basis of macro- and micro-morphology. Distribution data, descriptions and a taxonomic key to the species are provided. In *Khadia* we recognise the following species: *K. acutipetala* (N.E.Br.) N.E.Br., *K. alticola* Chesselet & H.E.K.Hartmann, *K. beswickii* (L.Bolus) N.E.Br., *K. borealis* L.Bolus and *K. carolinensis* (L.Bolus) N.E.Br.

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## INTRODUCTION

*Khadia* N.E.Br. is one of the few genera of the large, primarily southern African succulent plant family Mesembryanthemaceae Fenzl, which occurs in the north-eastern summer rainfall area of South Africa. Other mesem genera represented in this region include the widespread *Delosperma* N.E.Br. ( $\pm 30$  species), *Lithops* N.E.Br. (3 species), and *Frithia* N.E.Br. (1 species). *Khadia* occurs in three broad areas: 1, the Northern Province; 2, Gauteng and the North-West; and 3, Mpumalanga extending into northern KwaZulu-Natal (Figure 1). All known species of *Khadia* occur at altitudes above 1 400 m in quartzitic soils of the Soutpansberg Group, the Steenkampsberg Formation, the Magaliesberg Formation and the Witwatersrand Super-group.

A study of herbarium specimens of *Khadia* indicated obvious problems in species identification. The major reason for these problems is poor initial species diagnosis attributable to inadequate sampling of populations.

The intrinsic complexity of some of the taxa as well as the outdated revisionary status of the genus contributed to the confusion. In this paper we have attempted to facilitate identification of species, improve species diagnosis, bring systematics up to date and examine the characteristics of the species accommodated in the genus and hence its integrity. We have provided distribution data, descriptions and a taxonomic key to the species. A recent discovery by Pieter Winter (P. Winter in prep., University of the North, Sovenga) suggests the existence of an undescribed taxon, closely allied to *K. borealis* L.Bolus, which is not included in this paper.

## HISTORICAL BACKGROUND

*Mesembryanthemum acutipetalum* N.E.Br. was the first species to be described in this group (Brown 1908). A note on the label of the type specimen detailed its use in making 'Khadi' (see below under USES), prompting N.E. Brown, in his dismantling of *Mesembryanthemum* L., to formulate the genus name *Khadia* in a taxonomic key to genera of the 'Mesembryanthema' (Brown 1930). By 1931, four species were assigned to the newly circumscribed *Khadia*: *K. acutipetala* (N.E.Br.) N.E.Br., *K. nationiae* (N.E.Br.) N.E.Br., *K. beswickii* (L.Bolus) N.E.Br., and *K. nelsonii* N.E.Br., all of which were discovered in the surroundings of Johannesburg (Brown

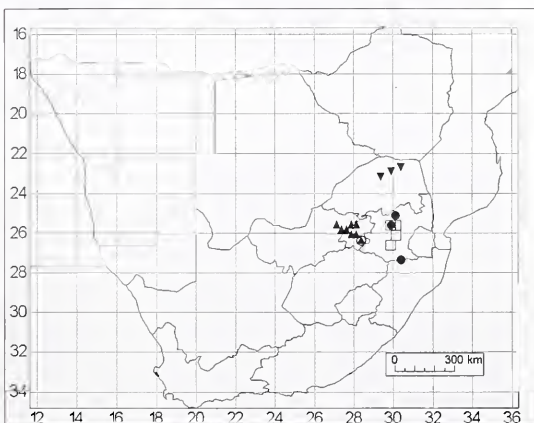


FIGURE 1.—Known distribution of: *Khadia acutipetala*, ▲; *K. alticola*, ●; *K. beswickii*, ◻; *K. borealis*, ◆; *K. carolinensis*, ▽.

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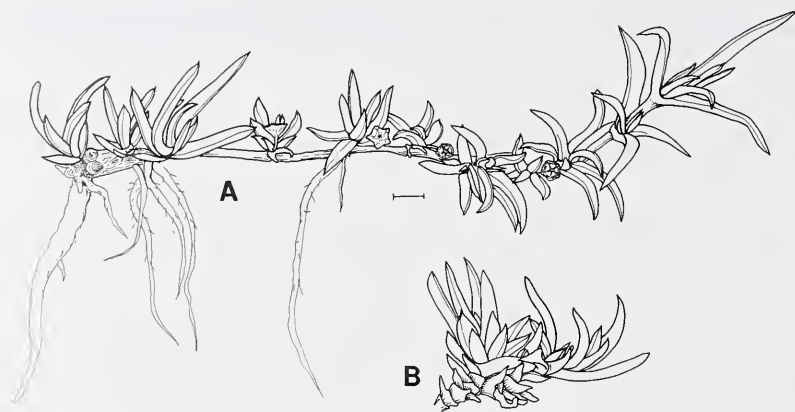


FIGURE 2.—Growth forms of *Khadia* spp.: A, *K. borealis*: long internodes distinguish this species from all other *Khadia* species; B, *K. alticola* with tightly packed leaf bases and internodes not visible. Scale bar: 10 mm. Drawn by P. Chesselet.

1931). Bolus' (1936) overview of the genus included six species names, with *K. carolinensis* (L.Bolus) N.E.Br. and the then newly described *K. borealis* completing the picture. A short overview of *Khadia*, highlighting *K. beswickii* and providing a key to species, appeared in *The Flowering Plants of Africa* (Bolus 1958). Treatment of the genus in Jacobsen (1960, 1981) was largely based on published information. No further attempts were made to resolve taxonomic problems in this genus until Chesselet & Hartmann (1995) described *K. alticola*.

The identity of *K. beswickii* has been problematic since its original description from a plant cultivated in an Eastern Cape garden. The name has been misapplied in herbarium identifications to the recently described *K. alticola* (Chesselet & Hartmann 1995) and to *K. acu-*

*tipetala* specimens with six sepals. Bolus (1922) distinguished *K. beswickii* from *K. acutipetala* by its nearly isophyllous habit, glaucous leaves, six-partite flowers and pale rose petals. Brown (1931) was not able to distinguish *K. beswickii* from *K. acutipetala* in dried specimens in flower, and emphasized that distinction is possible only when fruit are available. He described the capsule of *K. beswickii* as similar to that of *K. acutipetala* but with only six locules. Brown (1926) placed *K. beswickii* in synonymy under *K. acutipetala* but reinstated it five years later (Brown 1931). Bolus (1936) considered *K. beswickii* and *K. nationiae* (N.E.Br.) N.E.Br. to be close allies of *K. acutipetala* but emphasized that the number of sepals on all flowers of the type of *K. beswickii* was six. Without live material at his disposal, Brown used the more conspicuous 'streaks

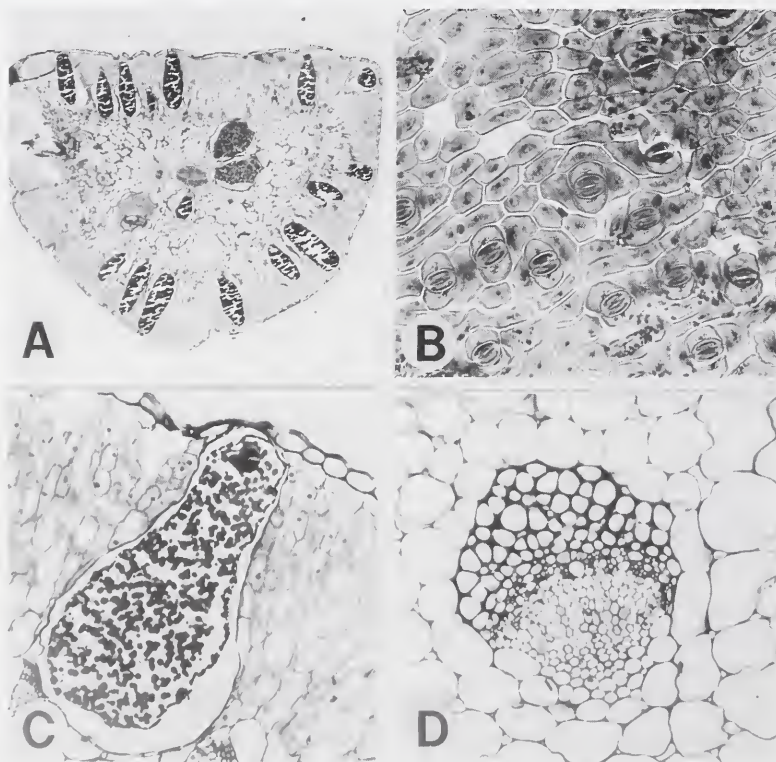


FIGURE 3.—Leaf anatomy of *Khadia*: A, *K. borealis*, Chesselet & Burgoyne 3, PRE: *vs* leaf epidermal layer with palisade layer and parenchymatous cortex, both containing enlarged idioblast cells filled with tannins,  $\times 17$ . B, D, *K. carolinensis*, Chesselet & Burgoyne 5, PRE: B, leaf surface scrape showing anomocytic stomata,  $\times 170$ ; D, detail of collateral vascular bundle,  $\times 170$ . C, *K. alticola*, Chesselet & Burgoyne 4, PRE: detail of tannin-containing subepidermal idioblast commonly known as 'pellucid dots',  $\times 170$ .



and dots', possibly phlobaphenes, on the dried petals of *K. nationiae* to distinguish it from *K. acutipetala*, and seems to have considered this characteristic sufficient to keep them distinct. He later distinguished *K. nationiae* from *K. acutipetala* and *K. beswickii* by its longer leaves abruptly rounded to a point in side view, the longer pedicel and the longer, leaf-like calyx lobes (Brown 1931).

*K. nelsonii* is known from a single collection and Brown (1931) in describing it, considered it to be very similar to *K. acutipetala*. This specimen was collected near Boksburg, on the outskirts of Johannesburg. Its ecological requirements were thought to differ from those of *K. acutipetala* as it had been found in a 'strong, greasy, loam country'. It displayed elongate growth with longer leaves, two longer leaf-like sepals, and six stigmata.

*K. borealis* is the northernmost ranging species in the genus. It was distinguished by its elongate branches with long internodes, and the absence of a closing body in the capsule (Bolus 1936). Until recently, this species had not been collected since its discovery in the 1930s. The new taxon of P. Winter mentioned in the introduction, closely resembles *K. borealis*, but lacks the distinctive long internodes on the branches.

#### TAXONOMY

**Mesembryanthemaceae** Fenzl in *Annalen des Wiener Museums der Naturgeschichte* 1: 349 (1836), emend. Herre & Volk in *Sukkulantenkunde* 2: 38 (1948).

**Ruschioideae** Schwantes in Ihlenfeldt, Schwantes & Straka in *Taxon* 11: 54 (1962), emend. H.E.K.Hartmann & Bittrich.

**Khadia** N.E.Br. in *The Gardeners' Chronicle* 88: 279 (in clave) (1930). Type species: *K. acutipetala* (N.E.Br.) N.E.Br. [= *Mesembryanthemum acutipetalum* N.E.Br.: 407 (1908)].

Perennial dwarf succulent, compact to mat-forming, more or less anisophyllous. *Rootstock* thickened, bearing  $\pm$  horizontal underground 'branches', divided at apices into branches with internodes mostly reduced and obscure or elongated up to 40 mm with adventitious roots at nodes (Figure 2A, B). *Leaves* opposite with 2 (3, in cultivation up to 4) new leaf growths per branch per season; connate at base, triquetrous distally with acuminate tips, semiterete basally and broader than thick, dark green or glaucous; subepidermal enlarged tanniferous cells (pellucid dots) concentrated along keel and margins of leaves, embedded in subepidermal palisade layer and in parenchymatous pith; stomata anomocytic; vascular bundles collateral (Figure 3). *Flowers* solitary, pedicellate. *Calyx* 5–6-lobed, length of calyx lobes variable. *Petals* white to deep magenta, with shades of pink. *Staminodes* filamentous, white to purple, forming a distinct cone in newly opened flowers, spreading and bending backwards in time. *Stamens*: filaments variable in colour and length; pollen grains tricolpate, exine structure semitectate; exine sculpture reticulate; muri thick, with supratectal spinules (Figure 4I). *Nectary* forming a dark green ring (lophomorphic). *Ovary* (4)5–11-locular,

upper surface convex or centrally depressed (Figure 5); placenta parietal; stigmata as many as locules, sometimes longer than filaments, adnate to upper surface of ovary. *Fruit* a loculicidal capsule with as many locules as ovary, reddish when young, dark brown later; pedicel persistent or breaking off, resulting in a tumble fruit; top of capsule raised in centre, or flat; base hemispherical to funnel-shaped; valves without wings but with enlarged rims, bases of expanding keels widely separated; covering membranes complete, rather firm, filled  $\pm$  with a whitish spongy tissue, with low rims at distal ends; closing device at distal rim of capsule reduced to a tiny bud or knob formed by placenta or by an outgrowth of expanding sheet over some protrusion from endocarp (Figure 6). *Seeds*  $\pm$  1 mm long; arrangement and orientation of testa cells of 'centrospermous' type, with sinuous or straight anticlinal walls, covered by granular or rod-shaped epicuticular ornamentation, micropylar end curved and elongated or short and straight (Figure 4A–H).

#### Key to species

- 1a Plants with some trailing stems and internodes up to 40 mm long ..... 4. *K. borealis*
- 1b Plants with internodes always shorter than leaves, mostly obscure:
  - 2a Fruit of a population mostly (6)8–10(11)-locular (at least 50 % of all fruit) ..... 1. *K. acutipetala*
  - 2b Fruit of a population mostly (5)6-locular (approximately 70 % of all fruit):
    - 3a Flowers white, opening in the afternoon .... 5. *K. carolinensis*
    - 3b Flowers pink to magenta, petal bases often paler, opening in sunlight:
      - 4a Leaves 25–40 mm long, glaucous ..... *K. beswickii*
      - 4b Leaves 11–14 mm long, dark green ..... 2. *K. alticola*

1. **Khadia acutipetala** (N.E.Br.) N.E.Br. in *The Gardeners' Chronicle* 89: 279 (1931).

*Mesembryanthemum acutipetalum* N.E.Br.: 407 (1908). Type: Gauteng, near Johannesburg, Turner 4448 (K, holo.).

*Khadia nationiae* (N.E.Br.) N.E.Br.: 279 (1931). *Mesembryanthemum nationiae* N.E.Br.: 46, 161, 162 (1926). Type: North-West, near Rustenburg, Nation s.n. (K, holo.).

Compact dwarf succulent, variable in degree of anisophyly; rootstock a thick tap root with underground branches, dense and obliquely to vertically orientated; aerial branches up to 100 mm long in old specimens, with persistent old leaf bases. *Leaves* triquetrous near acuminate tips and semiterete towards base, variable in length (15–35 mm) and breadth (4–6 mm), glaucous or dark green. *Flower* up to 40 mm diam. when open; pedicel 15–50 mm long. *Sepals* 5 or 6: two longer foliose ones with acutely pointed tips, one more rounded than the other, 11–19 mm long and 3 or 4 membranous ones with long pointed appendages at tips 5.5–10.5 mm long. *Petals* in 3 or 4 whorls, deep magenta to light pink; petaloid staminodes in a single whorl, pale pink,  $\pm$  8 mm long. *Androecium*: staminodes in 2 or 3 whorls; filaments white or pale pink, inner ones 4.0–7.5 mm long, middle ones 5.0–9.5 mm long, outer ones 8.0–9.5 mm long (Figure 4A), all papillate but outer ones only slightly so; anthers rich yellow; pollen faintly sweetly scented. *Ovary* with (6)8–10(11) locules, roofs of locules rising sharply; stigmata as many as locules, subulate, 3–8 mm long, growing with age, tips recurved. *Fruit* 8–12 mm diam. with flat-

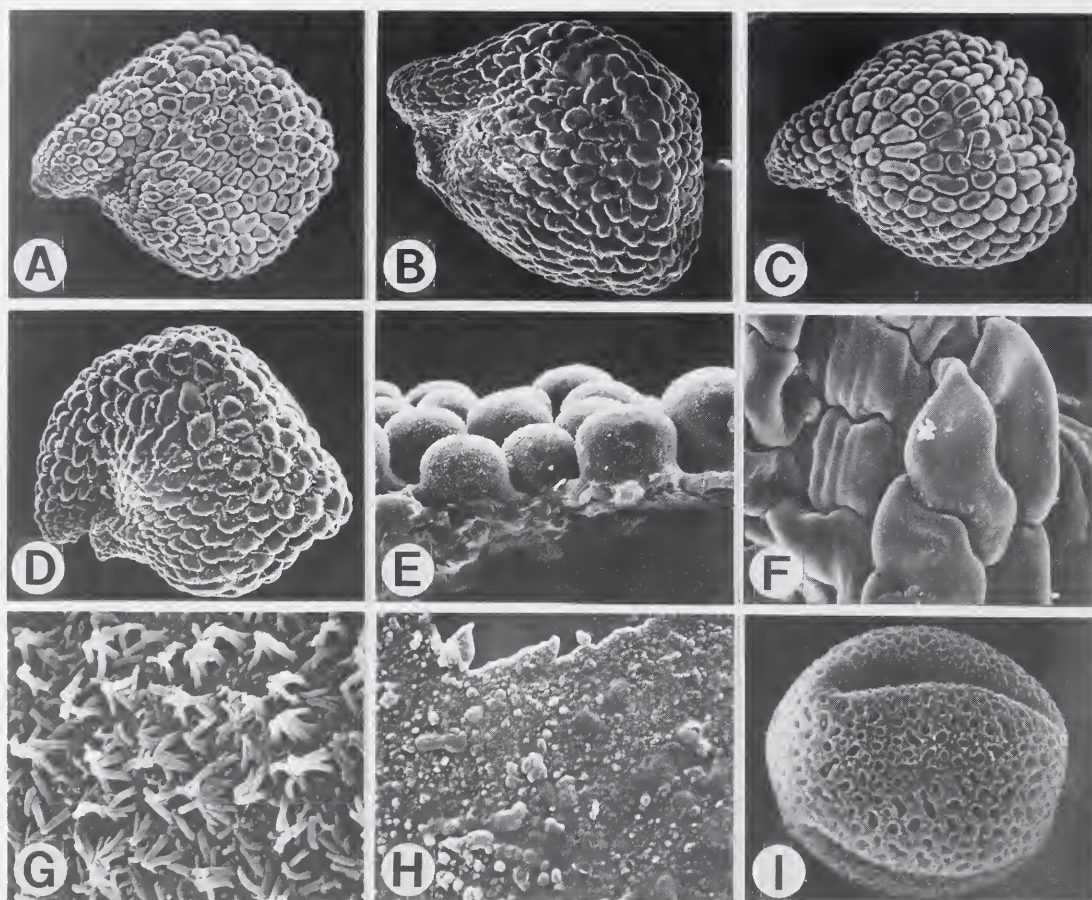


FIGURE 4.—Micromorphological characters of the seed (A–H) and pollen (I) of *Khadia*: A, *K. acutipetala*, Chesselet & Burgoyne 1, PRE,  $\times 46$ ; B, *K. alticola*, Chesselet & Burgoyne 4, PRE,  $\times 41$ ; C, *K. borealis*, Chesselet & Burgoyne 3, PRE,  $\times 53$ ; D, *K. carolinensis*, Chesselet & Burgoyne 5, PRE,  $\times 34$ ; E, *K. acutipetala*, Chesselet & Burgoyne 1, PRE,  $\times 256$ ; F, *K. beswickii* Ross Frames 17256, BOL,  $\times 277$ ; G, *K. borealis* Chesselet & Burgoyne 3, PRE,  $\times 2705$ ; H, *K. carolinensis*, Chesselet & Burgoyne 5, PRE,  $\times 2800$ ; I, *K. alticola*, Chesselet & Burgoyne 4, PRE,  $\times 2050$ .

tish, hemispherical, smooth-walled, shallow undersurface and a prominent raised lid; placenta parietal, extending to base of capsule; covering membranes opaque with recurved distal margins, raised centrally at columella or flat and folding centrifugally; valves wedge-shaped, curling outwards with ridge along centre of valve on inner surface; large phlobaphene-containing cells situated near tips of valves on inner side; 'closing bodies' minute, placental, or callous-like, with numerous funicles arising from them, or rod-like, and well defined; pedicel breaks off when fruit are ripe, forming tumble fruit, flat base facilitates upright position of fruit when detached from mother plant (Figure 6A–D). *Seeds* from capsules with centrally raised covering membranes mostly red, from capsules with flattish covering membranes mostly brownish, often quite pale; with straight testa cell walls, rodlet-shaped epicuticular sculpturing, micropylar end curved and elongated (Figure 4A, E).

On the Magaliesberg *K. acutipetala* occurs in rocky grassland near summits (1 600–1 700 m) in well-drained, loamy or gritty sand derived from Magaliesberg quartzites. Populations are found in full sun on gentle north-facing slopes in sparse grassland vegetation domi-

nated by *Tristachya biseriata*. Urbanisation threatens this species in a number of habitats—the Hospital Hill population near the city centre of Johannesburg has long since disappeared and the Northcliff Ridge populations in the suburbs of Johannesburg, are presently threatened by habitat destruction. *K. acutipetala* is, however, fairly abundant in existing nature reserves and other fortuitously protected areas in Gauteng (Figure 1).

Note: the *K. acutipetala* species complex is characterised by morphological variation between and within populations, particularly of the capsule, but also of leaf colour and shape, seed and flower colour, and length of foliose sepals. Although differences may seem quite striking, close examination of individuals reveals a continuous gradient of character combination, making it impractical to define groups.

Vouchers: Behr 781 (PRE); Bredenkamp 875 (PRE); Chesselet & Burgoyne 1, 2 (PRE).

2. *Khadia alticola* Chesselet & H.E.K.Hartmann in Aloe 32: 48 (1995). Type: Mpumalanga, Steenkampsberg, Hartmann & Chesselet 32729 (PRE, holo.!).



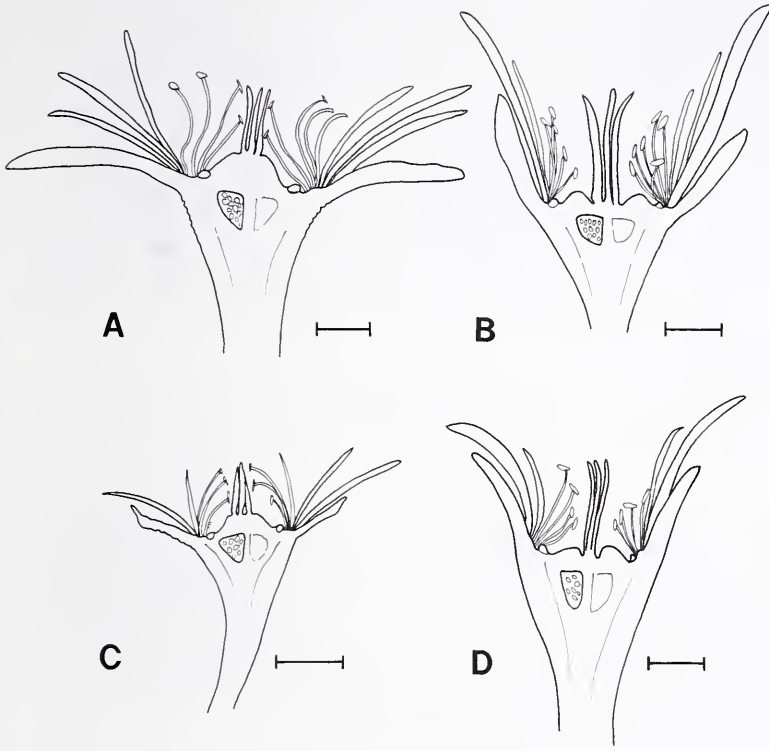


FIGURE 5.—Floral morphology of *Khadia*: A, *K. acutipetala*, Chesselet & Burgoyne 1, PRE; B, *K. alticola*, Chesselet & Burgoyne 4, PRE; C, *K. borealis*, Chesselet & Burgoyne 3, PRE; D, *K. carolinensis*, Chesselet & Burgoyne 5, PRE. Scale bar: 5 mm. No material of *K. beswickii* was available. Drawn by P. Chesselet.

Mat-forming, anisophyllous, succulent perennial with main tap root and multiple branching occurring just under soil surface, adventitious roots produced at nodes; new growth develops at periphery of mats anisophyllous. *Leaves* triquetrous, 8.8–16.7 × 5.3–6.8 mm, bright green to dark green; old leaf bases persist longer than in other *Khadia* species (Figure 2B); usually two leaf pairs per seasonal growth and a maximum of 3 in habitat; up to 4 in cultivation. *Flowers* up to 40 mm diam. when open. *Petals* pink fading towards base with age. *Sepals* 6. *Androecium*: filamentous staminodes present; outer row of filaments 4.5 mm long, middle row 2.3 mm long and inner row 1.6 mm long (Figure 5B). *Ovary* with 6 locules; stigmata as many as locules, 4.9–6.0 mm long; placenta basal to parietal. *Fruit* opening incompletely and not closing again completely; closing bodies very small and brown, spongy tissue only in distal third of covering membranes, ending in a rather sharp ledge (Figure 6E–G). *Seeds*: 15 or 16 seeds per locule; testa cells isodiametric to slightly elongate with sinuous anticlinal walls covered with granular epicuticular ornamentation; micropylar end straight, hilum aligned parallel just below it (Figure 4B).

*K. alticola* is common at altitudes above 2 000 m in Mpumalanga and KwaZulu-Natal in shallow, sandy, humus-rich soil pockets and crevices between rock plates (Figure 1). At the Steenkampsberg site it occurs among *Helichrysum galpinii* in bouldery patches together with the geophyte *Brachystelma stellatum*, as well as grasses and forbs. These eastern populations are exposed to a high rainfall regime and mists.

Vouchers: Archer 1050 (PRE); N.J. Devenish 692 (PRE); Hartmann & Chesselet 32729 (PRE); Hilliard & Burt 9173 (BOL).

### 3. *Khadia beswickii* (L.Bolus) N.E.Br. in The Gardeners' Chronicle 89: 279 (1931).

*Mesembryanthemum beswickii* L.Bolus: 124 (1922). Type: Gauteng, near Johannesburg, *Beswick* NBG 218/20 (BOL, holo.).

*Khadia nelsonii* N.E.Br.: 279 (1931). Type: Gauteng, Witte Koppies near Boksburg, *Nelson* s.n. (K, holo.).

Mat-forming, anisophyllous, succulent perennial with short root system. *Leaves* weakly, triquetrous, roundish below, glaucous. *Flowers* with petals pink, white at base, often quite pale. *Fruit* with 6 locules, base of capsule bell-shaped and top low, rounded; rims of valves turned backwards, covering membranes completely spongy, distal closing ledge very inconspicuous to absent; closing body consisting only of placenta and a layer of expanding sheet tissue. *Seeds* with anticlinal walls of testa cells sinuous (Figure 4F); testa cells covered with granular epicuticular ornamentation.

*K. beswickii* is known from Nigel on the East Rand in Gauteng where it was collected in 1942 by A.A. Mauve at two localities on outcrops of the Witwatersrand Supergroup (Figure 1). The first, on the north side of the Spaarwater Dam, where it occurred together with *Lithops lesliei*, is now inaccessible due to the establishment of an informal settlement at the site. Whether these plants have survived there is uncertain. Specimens were collected by H.E.K. Hartmann at this site during the 1980's. At the second locality, outside Nigel, on the road

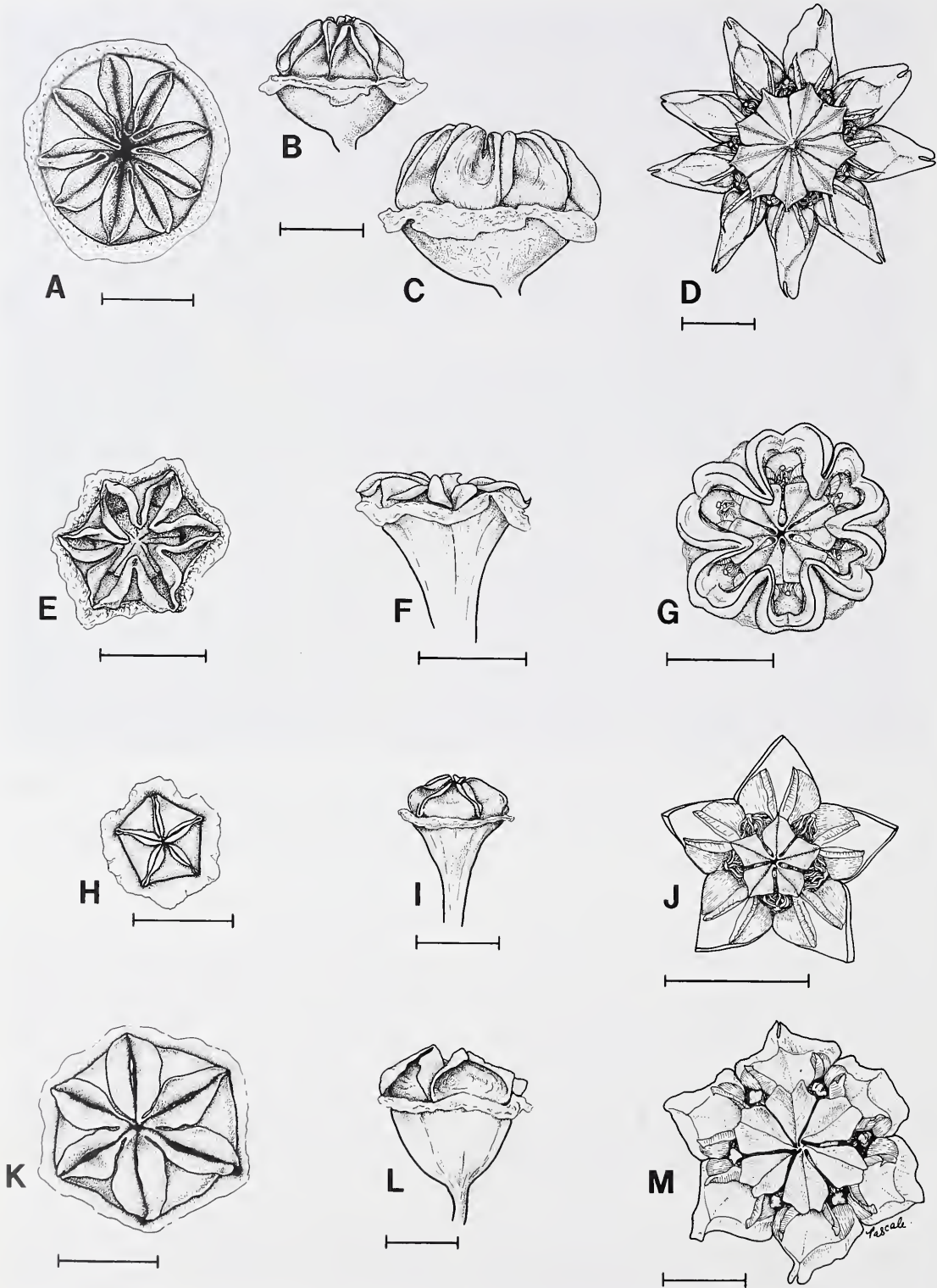


FIGURE 6.—Capsule morphology of *Khadia*: A–D, *K. acutipetala*, Chesselet & Burgoyne 1, PRE; E–G, *K. alticola*, Chesselet & Burgoyne 4, PRE; H–J, *K. borealis*, Chesselet & Burgoyne 3, PRE; K–M, *K. carolinensis*, Chesselet & Burgoyne 5, PRE. Scale bar: 5 mm. No material of *K. beswickii* was available. Drawn by P. Chesselet.

to Balfour, we noted large holes in microhabitats where plants may have grown, indicating possible harvesting. The species may be under threat of extinction, or extinct. Unlike the other *Khadia* species, which have been introduced into cultivation, live plants of this species were not available for study or propagation.

Vouchers: *Mauve s.n.* (PRE). *Ross Frames 17256* (BOL, PRE).

4. *Khadia borealis* L.Bolus in Notes on *Mesembryanthemum* and allied genera 3: 6 (1936). Type: Northern Province, Ventersdorp Farm, *Crundall s.n.* (BOL, lecto!, here designated); Northern Province, Zoutpansberg, Franzhoek Farm, *Vogts s.n.* BOL 21638 (BOL, paralecto!).

Perennial, slightly anisophyllous succulent with two kinds of branches: 1. creeping growth with rosettes at nodes on branches with distinct internodes, 15–40 mm long; and 2. tufted growth in branches where internodes are reduced; old leaf bases persisting; root system with thick tap roots and adventitious roots arising at nodes (Figure 2A). *Leaves* trigonous in cross section, with pellucid dots concentrated along margins, glaucous, dark green, leaf tips taper abruptly into hyaline point; leaf pairs curve in same direction. *Flowers* small,  $\pm 15$  mm diam. *Petals* white or pink. *Calyx*: with 5 sepals, 2 long and 3 short with membranous margins. *Androecium*: petaloid staminodes present; filaments in 3 rows, outer, 3.5–5.0 mm long, papillate or epapillate, middle,  $\pm 3.6$  mm long, inner, 2.1–2.7 mm long (Figure 5C); nectary dark green, continuous and crenulate. *Ovary* with (4)5–(7)8 locules, stigmata as many as locules,  $\pm 3.5$  mm long. *Fruit* with lower part distinctly concave, top rather low, rims recurved, placenta forms protrusions or placental 'closing body', closing ledges present (Figure 6H–J). *Seeds* orange; testa cells more or less isodiametric to elongate with smooth, convex periclinal walls; anticlinal walls straight; epicuticular ornamentation consisting of rodlets; micropylar end elongate with hilar bulge small and indistinct.

In the Northern Province, the creeping *K. borealis* grows in shallow soil pockets along flat lying strata within the mist belt at approximately 1 400 m, near the summit of the Soutpansberg (Figure 1). It grows in full sun, in grassland vegetation.

Vouchers: *Chesselet & Burgoyne 3* (PRE). *Hahn 430, 539, 604* (Herb. Sout.).

5. *Khadia carolinensis* (L.Bolus) L.Bolus in Notes on *Mesembryanthemum* and allied genera 3: 6 (1936).

*Rabiea carolinensis* (L.Bolus) N.E.Br.: 53 (1931). *Mesembryanthemum carolinense* L.Bolus: 128 (1922). Type: Mpumalanga, Carolina, F.A. Rogers s.n. NBG 1833/17 (BOL, lecto!, here designated); Mpumalanga, Carolina, C.L. Leipoldt s.n. NBG 2819/17 (BOL, paralecto!).

Plants very slightly anisophyllous, forming large mats up to 1 m diam.; thick tap roots branching underground; stems thickly covered with dead leaf bases. *Leaves* subterete to outside, flattened on inner side, dark green. *Flowers*  $\pm 35$  mm diam., opening in afternoon; pedicels  $\pm 10$  mm long. *Petals* white (at times recorded as yellow owing to slight yellow tinge on outer surface), in 3 rows,

$\pm 10$  mm long. *Calyx* with 6 sepals, foliose and membranous, of similar length. *Androecium*: petaloid staminodes  $\pm 6.5$  mm long; stamens  $\pm 7$  mm long, in 3 tiers, outer epapillate  $\pm 8$  mm, middle papillate at base  $\pm 6$  mm, inner papillate 5 mm (Figure 5D). *Ovary* with 6 locules; stigmata as many as locules, subulate,  $\pm 7.5$  mm long, protruding beyond stamens, orange. *Fruit* with broad closing ledges and tent-shaped covering membranes; closing bodies large (Figure 6K–M). *Seeds*: testa cells with sinuous anticlinal walls; epicuticular ornamentation granular; micropylar end curved inwards towards upward curving hilar bulge (Figure 4D, H).

*K. carolinensis* is plentiful in sandy loam among quartzite rocks near Carolina in Mpumalanga, at altitudes of  $\pm 1\ 740$  m (Figure 1).

Vouchers: *Burgoyne 2388* (PRE); *Du Toit 390* (PRE); *Sirey 3426* (PRE).

## DISCUSSION

The growth form of *Khadia*, with a thick underground, upward-branching root system and a mat of succulent leaves above ground is not uncommon in other mesem genera such as *Hereroa* (Schwantes) Dinter & Schwantes and *Ebracteola* Dinter & Schwantes. *Khadia* is formally classified in the now outdated subtribe *Nananthinae* Schwantes, comprising plants forming 'rosettes or clumps', and including *Nananthus* N.E.Br., *Aloinopsis* Schwantes, *Titanopsis* Schwantes, *Khadia* N.E.Br. and *Rabiea* N.E.Br. (Herre 1971). Bolus (1958) considered *Khadia* to be closely allied to typical *Ruschia* Schwantes, differing in the variable number of stigmata and in the absence of bracts, and in some species by the 'placental tubercle'. The character combination present in *Khadia* makes its systematic placement difficult amongst the ruschioid genera (Hartmann 1991, 1993). It was tentatively placed in the *Ruschia*-Group and thought to be closest to *Acrodon* (Hartmann 1991), which is endemic or near endemic to the Little Karoo Centre (Hartmann 1994). Recent examinations of the 'closing body', the structure that blocks the opening of the locules in the capsules of this genus, have shown that it is not homologous with such structures recognised in other genera (Chesselet & Hartmann 1995). In a detailed study of capsules of the 'Mesembryanthema', Hartmann (1988) distinguished endocarpal closing bodies from similar structures derived from the placenta. In the case of *Khadia* the so-called 'closing bodies' are of placental or more complex composition. Due to the unusual nature of this type of closing device, further investigation is required before a decision can be taken regarding the systematic affinities of *Khadia*. Our present postulate, based on capsule characteristics, is that its affinities may lie with *Ebracteola*.

Although the genus concept of *Khadia* has not been critically evaluated, it is generally considered sufficiently distinct from that of other mesem genera. Internal features of the capsule have been highlighted as being typical for the genus (Chesselet & Hartmann 1995). The composition of the 'closing body' is the single most important of these features and has been used to distinguish species in the group. In her studies of leaf anatomy in the mesems, Dupont (1968) suggests that in a well-



defined genus all species have the same type of stomata, or proportions of the different types. In *Khadia* all species have anomocytic stomata, which is the primitive state in the mesems (*K. beswickii* was not investigated anatomically as we had no fresh material). Nevertheless, there is no single apomorphy that can serve to delimit *Khadia*. Hence the cohesion of *Khadia* is unashamedly one of convenience, based on shared characteristics of uncertain homology and favoured by the need for taxonomic stability. Recently, Chesselet & Hartmann (1995) separated *Khadia* into two groups: Group 1 which included *K. acutipetala* and Group 2 which included *K. beswickii*, *K. borealis* and *K. carolinensis*. Data presented here suggest otherwise (Table 1). We propose two or possibly three groups which may represent subgenera or even separate genera: 1, The *K. acutipetala* species complex excluding or including 2, *K. borealis*, and 3, the distinct eastern group which includes *K. beswickii*, *K. alti-*

*cola* and *K. carolinensis*, and is united by features of the flower, capsules and seed. *K. borealis* shares seed characters, particularly the shape and ornamentation of testa cells, with *K. acutipetala* but the capsule of *K. borealis* is distinct (Figure 6).

Flower, fruit and seed morphology have been useful sources of taxonomic information at the species level and in establishing informal groups within *Khadia*. Further investigations into capsule and floral anatomy, as well as chemical characterisation may elucidate some of the problems of delimitation outlined here but are unlikely to make taxonomic decisions any easier.

#### USES

'Khadi' is a Tswana/South Sotho name for beer brewed traditionally using the fleshy roots of a variety of

TABLE 1.—Character distribution in *Khadia*

Characters/ Taxa	<i>K. alticola</i>	<i>K. beswickii</i>	<i>K. carolinensis</i>	<i>K. acutipetala</i>	<i>K. borealis</i>
<b>Growth form</b>	mat-forming	mat-forming	mat-forming	mat-forming	mat-forming and creeping
<b>Relative length of internodes</b>	shorter than leaves, not visible	shorter than leaves, not visible	shorter than leaves, not visible	shorter than leaves, not visible	longer than leaves, up to 40 mm long
<b>Petal colour</b>	pink	pale pink, white at base	white, with yellowish undersurface	pink to magenta	white or pink
<b>Flowering time</b>	in sunlight	in sunlight	in the afternoon	in sunlight	in sunlight
<b>Number of sepals</b>	6	6	6	5 or 6	5
<b>Nature of pedicel</b>	pedicel remains: stalked fruit	pedicel remains: stalked fruit	pedicel remains: stalked fruit	pedicel disintegrates: tumble fruit	pedicel remains: stalked fruit
<b>Number of locules</b>	6	6	6	(6)8–10(11)	(4)5–7(8)
<b>Shape of capsule undersurface</b>	funnel-shaped to hemispherical	bell-shaped	hemispherical	hemispherical	funnel-shaped, sides concave
<b>Capsule lid</b>	flat	flat	flat	raised	flat
<b>Valves of capsule when wet</b>	do not open completely	?	do not open completely	open completely by bending backwards	open completely by bending backwards
<b>Valves closing upon drying</b>	do not close completely	?	close almost completely	close completely	close completely
<b>Covering membranes</b>	spongy in distal parts	spongy throughout	spongy tissue comprising broad-based ledge or a narrow closing bulge	opaque with recurved distal margins, may be raised centrally or flat and folded centrifugally	without spongy tissue, with a distinct closing ledge
<b>Structure of 'closing bodies'</b>	small brown, placental/endocarpal	erect rodlet	large and white placental/endocarpal	variable: minute to well defined; placental (rather than endocarpal) protrusions	placental protrusions
<b>Relative length of stigmata</b>	overtopping stamens	?	overtopping stamens	± same length as stamens	± same length as stamens
<b>Micropylar end of seed</b>	straight	?	curved	curved, elongated	curved, elongated
<b>Hilum (seed)</b>	relatively large	?	relatively large and curved	relatively small	relatively small
<b>Shape of anticlinal walls of testa cells (seed)</b>	sinuous	sinuous	sinuous	straight	straight
<b>Ornamentation of testa cells (seed)</b>	granules	granules	granules	rodlets	rodlets



taxa. A number of mesem species, including *Delosperma mahonii* (N.E.Br.) N.E.Br. and *Trichodiadema stellatum* (Mill.) Schwantes are reported to have been used in brewing alcoholic beverages (Juritz 1906; Brown 1926). Researching the beer making process, Juritz (1906) predicted that any starchy root would suffice as long as mouldy dough could be made of it. It is of interest to note that brewing or possession of these beers was punishable in terms of the Liquor Law amendment act, No. 28 of 1898 (Juritz 1906). Whether the roots of *K. acutipetala* are still used today is uncertain. *Khadia* is reported to be used medicinally by Manyika people of the Umtali District of Zimbabwe (Watt & Breyer-Brandwijk 1962) suggesting the distribution of this genus beyond South Africa into Zimbabwe.

#### SPECIMENS EXAMINED

- Archer 1050 (2) PRE; 2093 (4) PRE.  
 Behr 781 (1) PRE. *Beswick s.n.* NBG 218/20 (3) BOL. *Bredenkamp* 875 (1) PRE. *Bryant D63, D79* (1) BOL. *Burgoyne* 2388 (5) PRE.  
*Chesselet & Burgoyne* 1, 2 (1) PRE; 3 (4) PRE; 4 (2) PRE; 5 (5) PRE. *Codd* 524 (5) PRE; *s.n.* PRE 55073 (2) PRE; *s.n.* (2) BOL. *Crundall s.n.* (4) BOL.  
*Devenish* 692 (2) PRE. *Du Toit* 390 (5) PRE.  
*Fuller* 83 (1) BOL.  
*Galpin* 21659, *s.n.* (5) BOL; *s.n.* NBG 1278/31 (1) BOL. *Gilfillan* 90 (1) PRE. *Gilmore* 237 (1) BOL.  
*Hahn* 430, 539, 604 (4) (Herb Sout). *Hardy* 441 (1) PRE. *Hartmann & Chesselet* 32729 (2) PRE. *Hilliard & Burt* 9173 (2) BOL.  
*Jacobsen* 756 (1) PRE.  
*Leendertz* 2462 (1) BOL; 7714 (1) PRE; 9166 (5) PRE. *Liebenberg* 12332 *S.U.G* (5) BOL; 12334, *s.n.*, *s.n.* (1) BOL.  
*Mauve s.n.* (3) PRE. *Mogg* 14778, 14902 (1) BOL. PRE.  
*Nation* 372 (1) BOL; *s.n.* (1) K. *Nelson s.n.* (3) K.  
*Obermeyer s.n.* (1) PRE.  
*Repton* 444 (1) PRE. *Rogers s.n.* NBG 1833/17 (5) BOL. *Rose Innes* 210 (1) PRE. *Ross Frames* 17256 (3) BOL. PRE.  
*Steyn* 839 (5) BOL. *Strey* 3426 (5) PRE.  
*Thode* A1317 (1) PRE. *Turner* 4448 (1) K. PRE.  
*Van Jaarsveld* 14234 (4) PRE. *Vogt s.n.* (4) BOL. *Vogts* 21534, *s.n.* (1) BOL; *s.n.* PRE 55056 (1) PRE.  
*Watson-Dobie* 414, *s.n.* (1) BOL.  
*Young* 3019, 3054 (1) PRE.

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FSA contributions 11: Zingiberaceae

R.M. SMITH\*

Editor's note: *Hedychium coronarium* and *Siphonochilus kirkii* have been added by Mrs C. Archer, with the author's consent.

Rhizomatous herbs; rhizome usually fleshy, sympodial. each element terminating in a leafy or flowering shoot. *Leaf shoots* with few to many blades, either arranged spirally and with tubular sheaths (Costoideae) or distichously arranged, sheaths then usually open on side opposite lamina (Zingiberoideae). *Inflorescence* occasionally surrounded by sterile bracts, terminal on leaf shoot or borne directly on rhizome at base of leaf shoot or remote from it. *Flowers* zygomorphic, hermaphrodite or (rarely) unisexual, solitary in axils of bracts or in cincinni, with or without bracteoles. *Calyx* tubular, often unilaterally split. *Corolla tube* usually slender; petals 3, often subequal. *Labellum*: (anterior staminode) often large and showy; lateral staminodes usually present, either as conspicuous petaloid organs (Zingiberoideae/Hedychieae) or as small subulate teeth or swellings (Zingiberoideae/Alpineae). *Fertile stamen* one only; anther more or less sessile or with a distinct filament; thecae parallel or slightly divergent, connective sometimes developing into an appendage (anther crest). *Ovary* inferior, unilocular with parietal placentation or trilocular, or incompletely so with axile placentation; style filiform, upper part usually held between thecae; stigma usually expanded. *Epigynous glands* (stylodes) forming erect outgrowths on top of ovary in Zingiberoideae; in Costoideae, three septal nectary glands arise towards top of ovary. *Fruit* a dehiscent capsule or fleshy berry. *Seeds* arillate.

Over 40 genera and about 1000 species occurring mainly in the tropics of the Old World but with some representatives in South and Central America. Four genera, all belonging to the subfamily Zingiberoideae, are found in the African continent but only one, *Siphonochilus* (tribe Hedychieae), is native in the FSA area. Three species of *Hedychium* (tribe Hedychieae) and *Alpinia zerumbet* (tribe Alpineae) have become naturalised in certain areas.

The Zingiberaceae is notable for its spice plants and includes ginger, *Zingiber officinale*; cardamom, *Elettaria cardamomum*; and turmeric, *Curcuma longa*. Cultivated races of *Curcuma* are common in the Indian markets of KwaZulu-Natal and are not infrequent in gardens; they are used medicinally or powder from the tubers is used as a cosmetic.

- 1a Inflorescence borne separately from leaf shoot; flowers purple-pink, blotched with yellow in centre of labellum, sometimes unisexual ..... 1. *Siphonochilus*
- 1b Inflorescence terminal on leaf shoot; flowers yellow and white or red and yellow, hermaphrodite:

- 2a Inflorescence erect; corolla tube 50–90 mm long, slender; lateral staminodes petaloid ..... 2. *Hedychium*
- 2b Inflorescence pendulous; corolla tube under 20 mm long; lateral staminodes reduced to small subulate teeth ..... 3. *Alpinia*

I. SIPHONOCHILUS

**Siphonochilus** J.M.Wood & Franks in Medley Wood, Natal plants 6,3: t. 560, 561 (1911a); J.M.Wood & Franks: 274 (1911b); B.L.Burt: 369, t. 1 (1982). Type species: *S. natalensis* J.M.Wood & Franks [= *S. aethiopicus* (Schweinf.) B.L.Burt].

*Cienkowskia* Schweinf.: t. 1 (1867), non Regel & Rach: 48 (1859).

*Kaempferia* subgen. *Cienkowskia* K.Schum.: 67 (1904).

*Cienkowskiella* Y.K.Kam: 8 (1980).

*Inflorescence* borne separately from leaves, sometimes precocious, long pedunculate or peduncle very short. *Flowers* usually hermaphrodite, rarely unisexual, each subtended by a bract; bracteoles absent. *Calyx* 3-lobed, unilaterally split. *Petals* linear-lanceolate. *Labellum* large, showy, connate with petaloid lateral staminodes for at least half its length. *Stamen*: anther crest petaloid, often longer than parallel thecae. *Stigma* cup-shaped or two-lipped. *Epigynous glands* short, stub-like. *Ovary* trilocular with axile placentation.

Distributed from KwaZulu-Natal northwards to Ethiopia and the Nile lands and across the continent to Nigeria and the Gambia; also in equatorial West Africa. About 20 species have been described but the genus is badly in need of revision and the number is probably rather less. Two species are recorded from southern Africa.

*Siphonochilus* was raised partly on account of the unisexual flowers found in *Kaempferia natalensis*. This in itself is insufficient to warrant generic distinction but recent research has shown the separation of the African species from *Kaempferia* to be entirely justifiable. Spearing & Mahanty (1964) report that the African plants have a basic chromosome number of 14, that of Asiatic *Kaempferia* is 11. Morphologically, *Siphonochilus* differs in the absence of bracteoles, and in having lateral staminodes that are connate to the labellum for about half their length, non-ciliate rimmed stigma and stub-like rather than needle-shaped epigynous glands.

Key to species

- Flowers on an elongated peduncle ..... 2. *S. kirkii*
- Flowers on very short peduncle concealed by basal bracts ..... 1. *S. aethiopicus*

\* Royal Botanic Garden, Edinburgh, UK.  
MS. received: 1985-03-14.

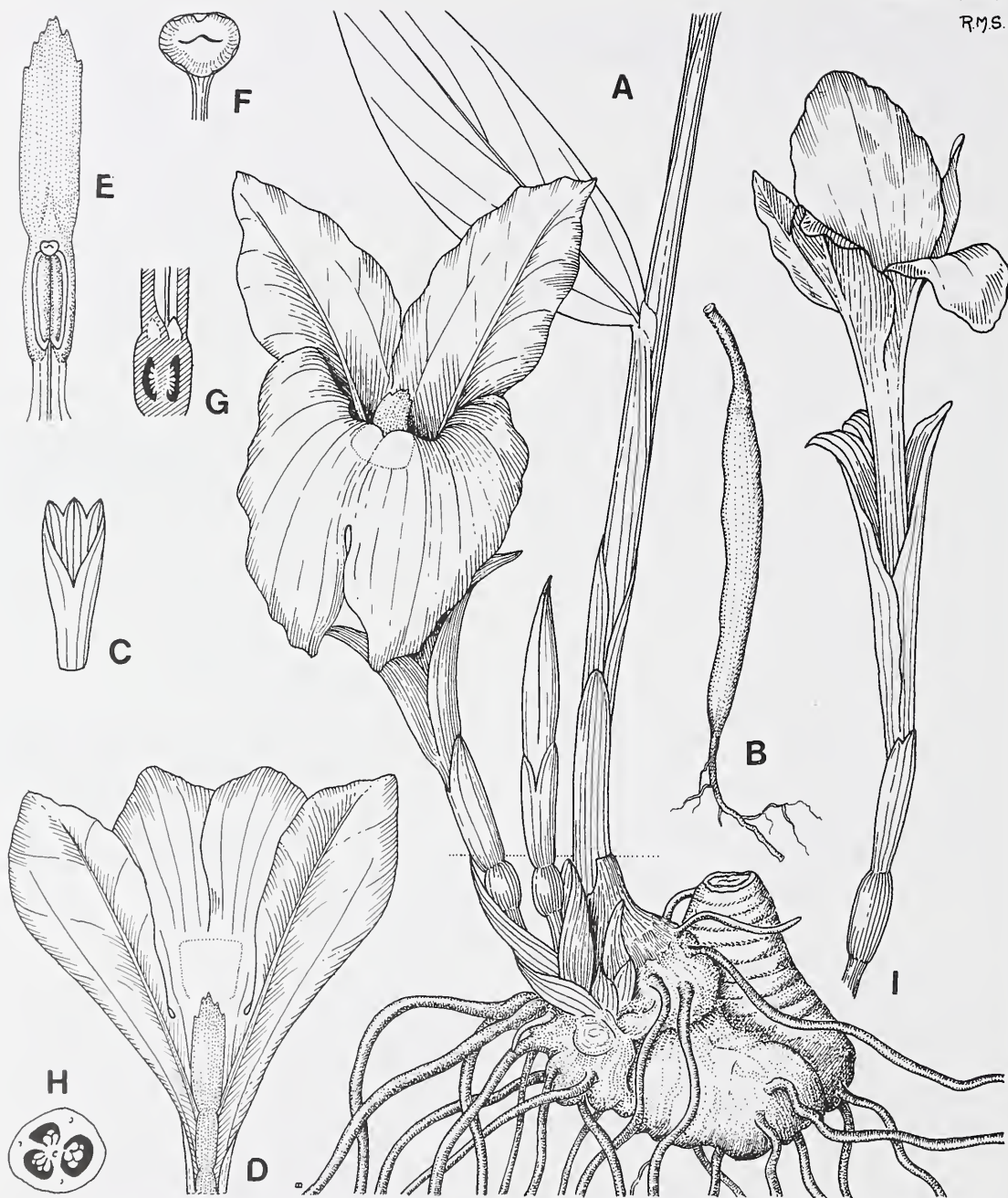


FIGURE 1.—*Siphonochilus aethiopicus*: A, habit,  $\times 0.8$ ; B, root tuber,  $\times 0.8$ ; C, calyx,  $\times 0.8$ ; D, labellum and lateral staminodes spread out showing position of stamen,  $\times 0.6$ ; E, stamen,  $\times 1.2$ ; F, stigma,  $\times 3.5$ ; G, l.s. of base of corolla tube and ovary, showing thickened walls of tube and epigynous glands,  $\times 1.2$ ; H, ovary in t.s.,  $\times 2$ ; I, female flower,  $\times 0.8$ . A–H, from Hilliard & Burt 6884A, Cult. R.B.G. Edinburgh; I, redrawn from Wood & Franks, t. 560.

1. *Siphonochilus aethiopicus* (Schweinf.) B.L. Burt in Notes from the Royal Botanic Garden Edinburgh 40: 372 (1982); Lock: 20 (1985). Syntypes: Ethiopia; am Khor el Sherif und bei Famaka in Fesoghlu, 23-v-1848, Cienkowski; an der Gandua zwischen Wochni und Metemme, 9-vi-1862, Steudner; bei Wochni im nordwest Abyss., 31-v-1862, 3-vi-1862, Steudner (K!).

*Cienkowskia aethiopica* Schweinf.: t. 1 (1867).

*Kaempferia aethiopica* (Schweinf.) Benth.: 642 (1883).

*K. ethelae* J.M.Wood: 94, t. 34 (1898); Wright: 314 (1913); Marloth: 167 (1915). Type: Cult. B.G. Durban, xi-1897, Wood 7667 (NH), originally from Mozambique, Vila de Manica (Massikessi), Benningfield.

*K. natalensis* Schlecht. & K.Schum. in K.Schum.: 72, fig. 10e, f (1904); J.M.Wood & Franks: 112 (1911c); Wright: 315 (1913); Marloth: 167, t. 53 (1915). Type: KwaZulu-Natal, Inanda, comm. viii-1879, Wood 544 (K!).

*Siphonochilus natalensis* (Schlecht. & K.Schum.) J.M.Wood & Franks: t. 560, 561 (1911a); J.M.Wood & Franks: 274 (1911b); B.L. Burt: 372, t. 1 (1982).

*Cienkowskiella aethiopica* (Schweinf.) Y.K.Kam: 10, t. 3 (1980).



Rhizome aromatic; fibrous roots bearing narrowly elongate tubers. *Leaf shoots* 300–1000 mm. *Leaves* 4–12, sessile, 300–400 × 50–90 mm (those at base of leaf shoot smaller), narrowly lanceolate, acuminate, glabrous; ligule 3–10 mm, membranous, entire; sheaths striate, glabrous. *Inflorescence* borne separately from leaf shoot, often precocious, basal part embedded in soil. *Flowers* 2–6, on a 10–20 mm bract-covered peduncle; floral bracts 25–30 × ± 15 mm, obtuse, glabrous; pedicels 10–20 mm long. *Hermaphrodite flowers*: calyx 20–30 mm, unilaterally split, shallowly 3-lobed, lobes rounded, sometimes with aristate point. *Corolla tube* white, 30–40 mm long, thick-walled. *Petals* white with pink tips, 60–80 mm long, lanceolate-acuminate. *Labellum*: purple-pink, yellow at throat in centre, free part ± 60–80 × 60–70 mm, bifid for up to  $\frac{3}{4}$  of its length, lower part connate with lateral staminodes for 50–60 mm and encircling stamen ('split-tube' of Wood & Franks); lateral staminodes (the free part) 60–80 × 40–50 mm, erect. *Stamen* 50–80 mm; filament 10–15 mm; thecae 15–20 mm, parallel; connective prolonged into a 30–50 mm petaloid, irregularly dentate reflexed crest. *Stigma* more or less cup-shaped. *Epigynous glands* 3–4 mm, stub-shaped, often embedded in fleshy corolla wall. *Ovary* 15 × 6 mm, glabrous, trilocular with axile placentation. *Female flowers*: calyx, corolla tube and petals as above. *Lateral staminodes* and labellum connate into an 80 mm closed tube; segments 4–6, 2 or 3, alternate ones 40 × 20 mm, oblong obtuse, the other 2 or 3, 40 × 5–7 mm, narrower. *Stamen* absent. *Gynoecium* as in hermaphrodite flower. *Fruit* unknown. Figure 1.

The description of the female flower is taken from Wood & Franks (1911a).

Occurs in Northern Province, Mpumalanga, Swaziland and KwaZulu-Natal (Figure 2). Widespread throughout tropical Africa. It seems likely that the species never occurred naturally in the *Flora* area but that it was introduced from tropical Africa and widely cultivated (Williams *et al.* 1996). In 19th century Natal, *S. aethiopicus* was often dug up and the tubers sold as horse medicine; nowadays it is found only in the vicinity of Zulu dwellings, where it was presumably originally planted. In traditionally Zulu practice the plant is used in the treatment of colds and chest complaints, to ward off snakes and lightning, and as a remedy for malaria. It is known as the Natal Ginger, *Sherungulu*, *Indungulu*.

Vouchers: Hilliard & Burtt 6884A (E); Holt, NH 28507 (NH); Medley Wood, NH 11250 (NH).

*S. aethiopicus* is a very polymorphic species, size, colour and depth of the lobing of the labellum may vary within a single population and considerable variation occurs in tuber length and in the size of the ligule.

The type plant of *Kaempferia natalensis* had only female flowers; Wood & Franks (1911a), when establishing *Siphonochilus*, recorded hermaphrodite flowers to be rare. In other respects the Natal plants cannot be separated from their more northerly counterparts.

2. *Siphonochilus kirkii* (Hook.f.) B.L.Burtt in Notes from the Royal Botanic Garden Edinburgh 40: 372

(1982); Lock: 15, t. 4 (1985). Type: Tanzania, cult. at Kew, *Kirk s.n.* (K, holo.).

*Cienkowskia kirkii* Hook.f.: t. 5994 (1872).

*Kaempferia kirkii* (Hook.f.) Wittm. & Perring: 57, t. 1364 (1892); Baker: 294 (1898); K.Schum.: 68 (1904).

*Cienkowskia kirkii* (Hook.f.) Y.K.Kam: 11 (1980).

*K. rosea* Baker: 295 (1898); F.W.Andrews: 255 (1956). Syntypes: Sudan, Schweinfurth 1946 (K, PRE!) and numerous other specimens from eastern Africa.

*K. montagui* F.M.Leight.: 57 (1932). Syntypes: Zimbabwe, nr Mazoe [= Mazowe], *Montagu s.n. sub NBG888/21* (NBG); *Wise s.n. sub NBG33/26* (NBG).

*Roots* bearing small fusiform tubers ± halfway along length. *Leaf shoots* 200–400 mm. *Leaves* 5–7, glabrous; lamina undeveloped in basal 1–3 or ovate to elliptic, acuminate, up to 170–310 × 55–100 mm, tapering at base into a false petiole up to 250 mm long (including leaf sheath); ligule obsolete; sheaths sulcate when dry. *Inflorescences* 1–4, borne separately from leaf shoot; 7–15(–20)-flowered; peduncle 200–350 mm long, terete, glabrous; bracts greenish, oblong to narrowly obovate, obtuse, the lower up to 65 × 20 mm, the upper very much smaller, up to 22 × 12 mm. *Flowers* hermaphrodite. *Calyx* campanulate, 8–15 mm long, shallowly 3-lobed, each lobe with a subterminal subulate projection ± 1 mm long. *Corolla tube* ± 8 mm long; petals narrowly obovate to narrowly oblong, acute, 22–26 mm long, whitish, tinged with green or mauve. *Labellum* 3-lobed, lateral lobes rhomboid, mauve, ± 30 × 20 mm, median lobe broadly spatulate, emarginate, ± 45 × 45 mm, mauve with a central yellow mark with or without a dark purple mark on each side. *Stamen* ± 25 mm long; thecae ± 5 mm long, curved; connective prolonged into oblong petaloid crest, ± 15 × 6 mm. *Ovary* ± 6 mm long, trigonous; stigma peltate. *Fruit* obovoid, trigonous, winged at angles, crowned with remains of calyx. *Seed* whitish, trigonous, ± 5.5 × 3.0 mm, with basal elaiosome.

Note: the above description is based on Lock (1985).

Occurs in the Caprivi Strip, Namibia (Figure 2). Widespread throughout tropical Africa.

Vouchers: Hardy 7110 (PRE); Killick & Leistner 3016 (PRE).

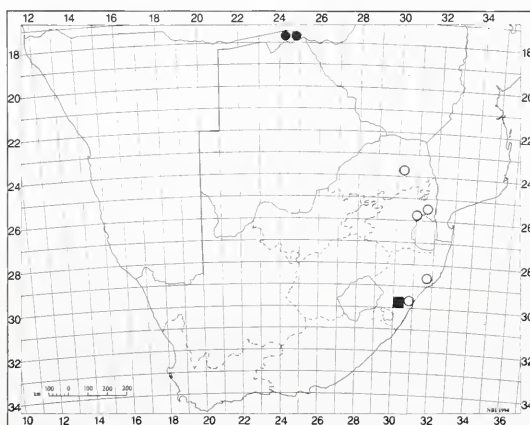


FIGURE 2.—Distribution of *Siphonochilus aethiopicus*, ○, *S. kirkii*, ●; and *Hedychium coronarium*, ■.

2. *HEDYCHIMUM* J.König

***Hedychium* J.König** in Retz., *Observationes botanicae* 3: 73 (1783); Benth. & Hook.f.: 642 (1883); K.Schum.: 40 (1904). Type species: *H. coronarium* J.König.

Plants up to 3 m tall. *Inflorescence* terminal on a frond-like leaf shoot; bracts broad and imbricating and concealing main axis or narrow and enfolding flowers. *Flowers* 1–6 per bract, each subtended by a tubular bracteole. *Corolla* tube long, slender, usually exceeding calyx. *Petals* strap-shaped. *Labellum*: narrowed at base with a conspicuous, usually bilobed limb; lateral staminodes petaloid; filament usually long and slender; anther connective ecristate. *Ovary* trilocular with axile placentation. *Fruit* globose or oblong, often bright red or orange within.

About 45 species, mainly eastern Himalayan, but a few known from southern India, Thailand, Malaysia and Indonesia. Several are widely cultivated throughout tropical and subtropical zones and are valued for their perfume and prolific flowers.

## Key to species

- 1a Bracts broad and imbricating, concealing main axis; petaloid parts white or yellow; filament white or yellow:  
 2a Flowers yellow; stamen longer than labellum ..... 2. *H. flavescens*  
 2b Flowers pure white, base of labellum usually yellow-green; stamen shorter than labellum ..... 1. *H. coronarium*  
 1b Bracts narrow, not concealing main axis; petaloid parts yellow; filament bright red ..... 3. *H. gardnerianum*

1. ***Hedychium coronarium* J.König** in Retz., *Observationes botanicae* 3: 73 (1783); Sims: t. 708 (1804); K.Schum.: 44 (1904). Type: Malaya, König s.n. (†).

Plant up to 3 m. *Leaves* sessile, up to 600 × 110 mm, lanceolate-acuminate, glabrous with a few silky hairs on and near midrib on abaxial surface; ligule papyraceous, white or brown, up to 30 mm high. *Inflorescence* up to 200 × 110 mm; bracts 40–60 × 20–30 mm, ovate-obtuse, subcoriaceous, green, overlapping, each subtending 2–6 flowers. *Flowers* white, intensely fragrant. *Calyx* tubular, unilaterally split, glabrous, hidden by bract. *Corolla tube* up to 70 mm; petals 3, linear-lanceolate, equal, declined. *Staminodes*: 30–50 mm, oblong-lanceolate; labellum ± 35 × 50 mm, usually yellow-green in centre, deeply 2-lobed. *Stamen* white, shorter than labellum; anther 12 mm long. *Ovary* glabrous, or slightly to densely hairy at flowering stage, 5 mm long. *Fruit* a capsule; seeds rounded, greyish, ± 5 mm long.

Note: the above description is partly based on Smith (1984), partly on Turrill (1914) and partly on new observations.

Vouchers: Rhind s.n. (PRE); Schlieben & Mendelsohn 12618 (cultivated) (PRE).

*H. coronarium* is widely cultivated in the tropics and subtropics. It has become naturalised in the Pietermaritzburg area (Figure 2), the seeds being dispersed by birds.

2. ***Hedychium flavescens* Roscoe**, *Monandrian* plants of the order Scitamineae: t. 50 (1825); Lourteig: 123 (1972). Type: Roscoe, Monandr. t. 50.

Plants 2–3 m high. *Leaves* sessile, up to 600 × 80 mm, lanceolate-acuminate, lightly pubescent below; ligule 10–20 mm, entire, pubescent. *Inflorescence* up to 200 × 80 mm; bracts 50 × 35 mm, broadly ovate, rather obtuse, membranous at margins, unevenly pubescent. *Flowers* yellow. *Calyx* up to 45 mm, pubescent, unilaterally split. *Corolla tube* ± twice length of calyx. *Petals* linear, ± 40 × 20 mm. *Labellum*: broadly obcordate, narrowed at base, bilobed above, 80 × 25 mm at broadest part; lateral staminodes 25–30 mm, spatulate. *Stamen* up to 40 mm long. *Ovary* silky pubescent. *Fruit* ?

*H. flavescens* is native to the eastern Himalayas. As a garden escape it has become naturalised in many countries and has been found in the Pietermaritzburg area.

3. ***Hedychium gardnerianum* Ker Gawl.** in *Botanical Register* 9: t. 774 (1 Feb. 1824); Roscoe: t. 62 (before 21 April 1824). Type: Hort. Liverpool, Sheppard.

Plants 2–3 m high. *Leaves* shortly petiolate, 240–400 × 100–150 mm, lanceolate-acuminate, glabrous; ligule 20–40 mm entire. *Inflorescence* up to 350 mm long; bracts 30–50 mm, convolute, remote. *Flowers* yellow. *Corolla tube* ± 50 mm long. *Petals* linear. *Labellum*: 25–30 × 10–20 mm, obovate, emarginate; lateral staminodes 30–35 mm long, narrowly oblanceolate; filament bright red. *Fruit* red within.

This very handsome species is also a native of the eastern Himalayas. The sweetly scented inflorescence is the largest found in *Hedychium*. It is naturalised around Kloof, inland from Durban.

3. *ALPINIA* Roxb.

***Alpinia* Roxb.** in *Asiatic Researches* 11: 350 (1810) nom. cons.; Benth. & Hook.f.: 648 (1883); K.Schum.: 308 (1904). Type species: *A. galanga* (L.) Willd.

*Catimbium* Lestib.: 346 (1841), non Juss. (1789).

*Languas* Small: 307 (1913).

Plants up to 120 mm tall, more usually 2–4 m. *Inflorescence* terminal on a frond-like leaf shoot. *Flowers* borne singly or in cincinni; bracts and/or bracteoles present or not. *Labellum*: often showy, lateral staminodes present as small subulate teeth or reduced to small swellings or absent; anther connective crested or not. *Fruit* usually spherical.

A large genus of at least 200 species widely distributed throughout SE Asia with representatives in Queensland and Japan.

1. ***Alpinia zerumbet* (Pers.) B.L.Burt & R.M.Sm.** in *Notes from the Royal Botanic Garden Edinburgh* 31: 204, t. 10 (1972). Type: Wendland, t. 19 (1798).

*Costus zerumbet* Pers.: 3 (1805).

*Zerumbet speciosum* Wendl.: 3, t. 19 (1798).

*Alpinia speciosa* (Wendl.) K.Schum.: 334 (1904), non (Bl.) D.Dietr.: 13 (1839).

*Catimbium speciosum* (Wendl.) Holtt.: 152 (1950).

Plants up to 3 m. *Leaves* sessile or shortly petiolate, up to 600 × 100 mm, lanceolate acuminate, margins pubescent, undersurface sometimes so; ligule pubescent. *Inflorescence* pendulous, up to 300 mm long, axis pubescent. *Flowers* white red and yellow, borne in 2-flowered cincinni; bracts absent; bracteoles glistening white with pink tips, open to base but encircling flower buds, quickly deciduous. *Corolla tube* shorter than 20 mm calyx. *Petals* white, dorsal much broader than laterals. *Staminodes*: labellum up to 40 mm long, broadly ovate, bifid at apex, yellow, mottled and striped with red; lateral staminodes slender, subulate, up to 10 mm long; anther massive, ecristate. *Ovary* densely pubescent. *Fruit* spherical, up to 20 mm diam., orange.

*A. zerumbet*, the Shell Ginger, is found in tropical gardens all over the world. It is probably truly native to NE India, Burma and Indo-China. It is reported to have escaped from gardens in the Hluhluwe area of Zululand.

#### Excluded species

*Kaempferia stenopetala* K.Schum. in Das Pflanzenreich Heft 20 Zing. 69 (1904); Wright: 314 (1913).

This name was based on an unlocalised collection from Natal (*Medley Wood 1942, K!*). It is almost certainly the Asiatic *K. rotunda* L. widely cultivated in the east for its medicinal properties, and presumably brought to Africa by the Indians.

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Notes on African plants

VARIOUS AUTHORS

CYPERACEAE

A NEW COMBINATION IN *ISOLEPIS*

Since its description by Nees von Esenbeck in 1836, the generic affinities of the small annual *Cyperus leucoloma* Nees from the Western Cape have remained unquestioned. Nees and subsequent authors compared and contrasted it with the superficially similar *C. tenellus* L.f. on account of its 'distichous' glumes. The type was not specified by Nees, but he stated that he had seen it 'in Herb. Reg. Ber.'. Boeckeler (1867/1868) cited a Bergius specimen in B, and Clarke (1897) and Kükenthal (1936) both cited *Bergius 174* in B. Fortunately it was possible to borrow this sheet (Figure 1).

Typification

The sheet consists of two specimens, one in the capsule (Figure 1A) without locality or collector information, and another (Figures 1B; 2), *Bergius 174*, collected at 'Prom. bon sp.'. Prof. Hiepko, Director of the Herbarium, B, is of the opinion that the two specimens were remounted onto one sheet in the latter half of the 19th century, when a larger size herbarium sheet was brought into use. It is highly likely that the specimen in the capsule is the one seen by Nees, as the note (Figure 1C) which was folded inside the capsule is almost certainly in Nees' handwriting (Burdet 1977: 189, 190). This specimen is therefore taken to be the holotype. The label (Figure 1D) of the specimen (Figure 1B) is written in Schlechtendal's hand, excepting the 'N. ab Es.' (P. Hiepko pers. comm.). K.H. Bergius was an apothecary and naturalist at the Cape from 1815 until his death in 1818, following which his specimens were sent to Berlin by Von Chamisso (Gunn & Codd 1981: 93). Schlechtendal was at that time and up until 1833 'supervisor of the public collection of herbs' (curator) at B (Hiepko 1987: 221).

Further evidence that this is the original sheet are the annotations thought to be by Boeckeler (Figure 1E), and those by Clarke (not shown) and Kükenthal (Figure 1F). Additionally, according to Hiepko (1987: 251), the types of *Cyperus s.l.* escaped the destruction during World War II because they had been moved to the basement of the Museum.

The correct generic placement of the species

There is currently much disagreement on the infrafamilial classification (at all levels) of Cyperaceae. However, it is generally agreed that *Cyperus s.str.* has distichous glumes and flattened spikelets, whereas *Isolepis* R.Br. has spiralled glumes and rounded spikelets. It

can be clearly seen that, while otherwise conforming exactly to Nees' description, the glumes in the holotype of *C. leucoloma* Nees appear to be subdistichous due to having been collected at a young stage and flattened by the collector. Glume scars on spikelet axes of dissected material (*Barker 243*) show clearly that the glumes are spirally arranged. *C. leucoloma* is undoubtedly a species of *Isolepis*: it is probably related to *I. incomptula* Nees which has a similar spikelet and glume morphology. The genus is currently under revision. Meanwhile the new combination is effected below.

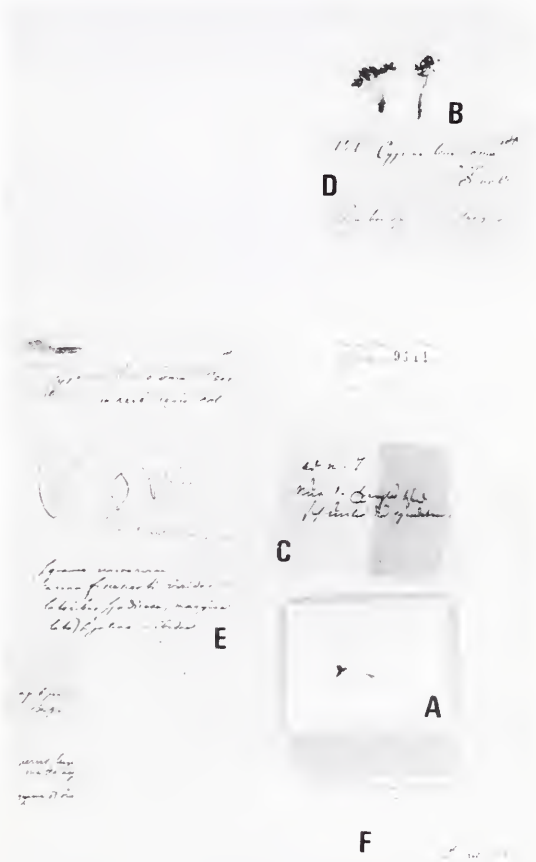


FIGURE 1.—*Isolepis leucoloma* (Nees) C.Archer. A, ?holotype; B, specimen; C, note in ?Nees' handwriting; D, label in Schlechtendal's handwriting; E, sketch annotated by ?Boeckeler; F, annotation by Kükenthal. Lowermost portion of sheet not shown. Photograph: R.H. Archer.

Hoek Peak, (–CC), *Stokoe s.n. sub SAM 59230* (SAM). 3418 (Simonstown): mountain at Kalk Bay, (–AB), *Levy's 831* (K).



FIGURE 2.—Enlargement of Figure 1B, *Bergius 174* to show morphology of species,  $\times 2$ . Photograph: R.H. Archer.

***Isolepis leucoloma* (Nees) C.Archer, comb. nov.**

*Cyperus leucoloma* Nees in *Linnaea* 10: 133 (1836); Kunth: 50 (1837); Boeckl.: 506 (1867/1868); C.B.Clarke: 566 (1894); C.B.Clarke: 165 (1897); Kük.: 298 (1936); Levyns: 99 (1950); Bond & Goldblatt: 39 (1984). Type: not specified [most probably: *Prom. bon. sp.*, *Bergius 174*] (B, specimen in capsule!).

*Specimens examined*

WESTERN CAPE.—3219 (Wuppertal): on road to Heuningvlei, (–AA), *Emdon 129* p.p. (NBG); Porterville, on plateau of Voorberg (above Dasklip Pass) on road to Forestry Centre, Zuurvlakte Farm, (–CC), *Barker 243* (PRE). 3318 (Cape Town): Malmesbury, (–BC), *Schlechter 16336* (K, P). 3319 (Worcester): Paarl Division, French

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ASTERACEAE

A NOTE ON THE *BRACHYLAENA DISCOLOR* COMPLEX

In their revision of the South African species of *Brachylaena*, Phillips & Schweickardt (1937) recognised nine species, including *B. uniflora* Harv., *B. transvaalensis* E.Phillips & Schweick. (a new species) and *B. discolor* DC. The key character by which they distinguished the latter three species was the number of flowers in the male capitula (1–3 in *B. uniflora*; 7–50 in *B. transvaalensis* and *B. discolor*). This is unfortunately not sufficient for identification purposes because female plants are not taken into account. *B. transvaalensis* was distinguished from *B. discolor* by the size of the capitula (less than 10 mm long in *B. transvaalensis* and over 10 mm long in *B. discolor*). Paiva (1972) reduced *B. transvaalensis* to a subspecies of *B. discolor* [*B. discolor* DC. subsp. *transvaalensis* (E.Phillips & Schweick.) Paiva] and divided *B. discolor* DC. subsp. *discolor* into two varieties (var. *discolor* and var. *mossambicensis* Paiva). He did not include *B. uniflora* in his publication as this species fell outside his study area, but a label on a specimen in PRE indicates that he recognised *B. uniflora* as a

separate entity. Hilliard & Burt (1971) studied these three species and came to the conclusion that they should be regarded as members of a complex comprising either a single species showing clinal variation in the number of flowers per capitulum, loosely linked to an ecological cline from coastal dunes to inland forest, or representing two species which have met and are now hybridising. They did find a general correlation between small, few-flowered capitula with short involucre and much-branched synflorescences, whereas larger capitula with longer involucre tend to correlate with less branched synflorescences. They did not find any conspicuous vegetative differences between these three species, a view supported by my studies of herbarium material. Hilliard (1977) did not agree with Paiva (1972) in the division of *B. discolor* into subspecies and varieties, a view also supported by Pope (1992) and myself. Cilliers (1993) published a synopsis of the genus *Brachylaena* in southern Africa. He followed Paiva in upholding the subspecies of *B. discolor* but sank *B. uniflora* Harv. under *B. discolor*

TABLE 1.—A summary of diagnostic features and distribution of three *Brachylaena* species

	<i>B. discolor</i>	<i>B. transvaalensis</i>	<i>B. uniflora</i>
<b>Involucre</b>			
♂ and ♀	large	small	small
Shape ♀	widely infundibuliform to cyathiform at base		
Shape ♂	globose to cyathiform		
Shape ♂ and ♀		globose to cyathiform	narrowly infundibuliform
♂ and ♀	distinct stalks	sessile or subsessile	slender
♂ and ♀	few scattered bracts	bracts extending to base of stalk	inner bracts narrowly triangular, acuminate, stiffly erect
Size ♀	(7–)10–18(–23) × (3.5–)5.0–10.0(–12.0) mm	(4.0–)5.5–7.0(–8.5) × (2.0–)3.0–4.5(–8.5) mm	(3–)4–7(–10) × 1–5 mm
Size ♂	(5.5–)6.0–13.0(–15.0) × (2.5–)4.0–6.0(–8.5) mm	(3.5–)4.0–6.5(–7.0) × (1.5–)2.5–3.5(–4.0) mm	2.5–4.0(–5.5) × 1–3 mm
<b>Life form</b>	shrubs or trees	large trees	shrubs or trees
<b>Habitat</b>	dune and coastal forests	inland medium altitude and Afro-montane forests	coastal forests
<b>Distribution</b>	coast of KwaZulu-Natal, Eastern Cape, few from Swaziland, Mpumalanga and Northern Province (Figure 4)	Northern Province, Mpumalanga, Swaziland, few from KwaZulu-Natal (Figure 4)	coast of KwaZulu-Natal, Eastern Cape, few specimens inland (Figure 4)

DC. subsp. *transvaalensis* (E.Phillips & Schweick.) Paiva. The illustration of *B. discolor* subsp. *transvaalensis* in Cilliers (1993: fig. 15), appears to depict a combination of *B. uniflora* and *B. transvaalensis*: the branch with leaves and female capitula (A) and the female capitulum (C) look like those of *B. uniflora*; the male capitulum (B) like that of *B. transvaalensis*. Pope (1992) in his treatment of the genus *Brachylaena* for the *Flora zambesiaca* area, recognised *B. discolor* without any subspecies and regarded *B. transvaalensis* as a separate species, as originally described by Phillips & Schweickerdt (1937). He did not mention *B. uniflora*, as this species did not fall within his study area. I agree with Phillips & Schweickerdt (1937) who kept the three species distinct and undivided, a view also subscribed to by Pope, as far as he studied the complex.

Not any of the above-mentioned authors used the shape of the involucre as a distinguishing character. The involucres of the three species are either infundibuliform, cyathiform or globose. It seems to be a constant character which can be used easily. Pope (1992) used the character of the capitula being stalked or not. This feature is not always easy to distinguish in South African material.

Table 1 gives a summary of the diagnostic features of the three species *B. discolor*, *B. transvaalensis* and *B. uniflora*. Using the shape of the involucre, they can generally be easily separated in the herbarium provided good fertile material of either sex is available. Distribution of the species (Figure 4) is listed in Table 1.

On the basis of the shape of the involucre, the three species can be separated as follows (measurements of involucre length include the stalk, where applicable, and width is measured across the widest part):

- 1a Involucre infundibuliform:**  
2a Male and female capitula small, synflorescences very dense, involucre of both male and female capitula narrowly infundibuliform, slender (Figure 3G–J), 2.5–4.0(–5.5) × 1–3 mm in male capitula and (3–) 4–7(–10) × 1–5 mm in female capitula; inner bracts

- narrowly triangular to almost linear, acuminate, stiffly erect; leaves oblanceolate to obovate, rounded or sometimes briefly acuminate at apex . . . . . 3. *B. uniflora*  
2b Female capitula large, mostly with distinct stalks with only a few scattered bracts, involucres of female capitula widely infundibuliform to cyathiform at base (Figure 3B), (7–)10–18(–23) × (3.5–)5.0–10.0(–12.0) mm; bracts narrowly ovate with apex acute and somewhat spreading, synflorescence less dense than in *B. transvaalensis*; leaves similar to those of *B. uniflora* but more constant in male than female plants . . . . . 1. *B. discolor*  
**1b Involucre globose to cyathiform:**  
3a Male capitula large, mostly with distinct stalks with only a few scattered bracts, involucres of male capitula (5.5–)6.0–13.0(–15.0) × (2.5–)4.0–6.0(–8.5) mm (Figure 3A); bracts narrowly ovate with apex acute, somewhat spreading, synflorescence less dense than in *B. transvaalensis*; leaves oblanceolate to obovate, rounded or sometimes briefly acuminate at apex but more constant in male than female plants . . . . . 1. *B. discolor*  
3b Male and female capitula small, mostly sessile or subsessile with involucral bracts extending to the base of the stalk, involucres (3.5–)4.0–6.5(–7.0) × (1.5–)2.5–3.5(–4.0) mm in male capitula and (4.0–)5.5–7.0(–8.5) × (2.0–)3.0–4.5(–8.5) mm in female capitula (Figure 3C–F), synflorescence very dense; leaves narrowly elliptic, acute and ± acuminate at apex but more constant in male than female plants . . . . . 2. *B. transvaalensis*

*Specimens examined*

Abbott 3958 (3) NH. Abrahams s.n. (1) PRE. Archibald 3632/32, 3690 (1) PRE. Aubrey s.n. NU34158, NU34172 (1) NU.  
Balkvill 372 (3) NU. Bayer 554 (1) NU. Bayliss BR1B 1499, 1516 (3); 1540 (1) PRE. Biegel 2258 (2) NU. Boocock 26 (3) PRE. Borchers 52 (2) PRE. D.J. Botha 654 (2) PRE. W.M. Botha 5286 (2) PRE. Bourquin 46 (2), 150 (1) NU. Breyer s.n. Tvl. Mus. 24388 (2) PRE. Britten 773, 1837, 2300, 2412 (1) PRE. Bruce 1 (1) PRE. Braumitt 12457 (2) PRE. Bruton 12 (1) PRE. Burger 525 (2) PRE. Burt Davy 2392 (1) PRE.  
Coleman 335 (3) NH. Comins 1255A (1) PRE. Compton 26061, 26994, 29070, 29073 (2) PRE. Cooper 1240 (1) PRE. Culverwell 961, 975 (1) PRE. Cunningham 856 (3) NU.  
Davis 82 (3) NH. De Winter 8359a (1) PRE. Dlamini s.n. PRE31785, PRE31787, PRE43310 (2) PRE. Du Toit 1265 (1) NH, PRE.  
Edwards 1529 (3) NU, PRE. Evans 5398 (2) PRE.



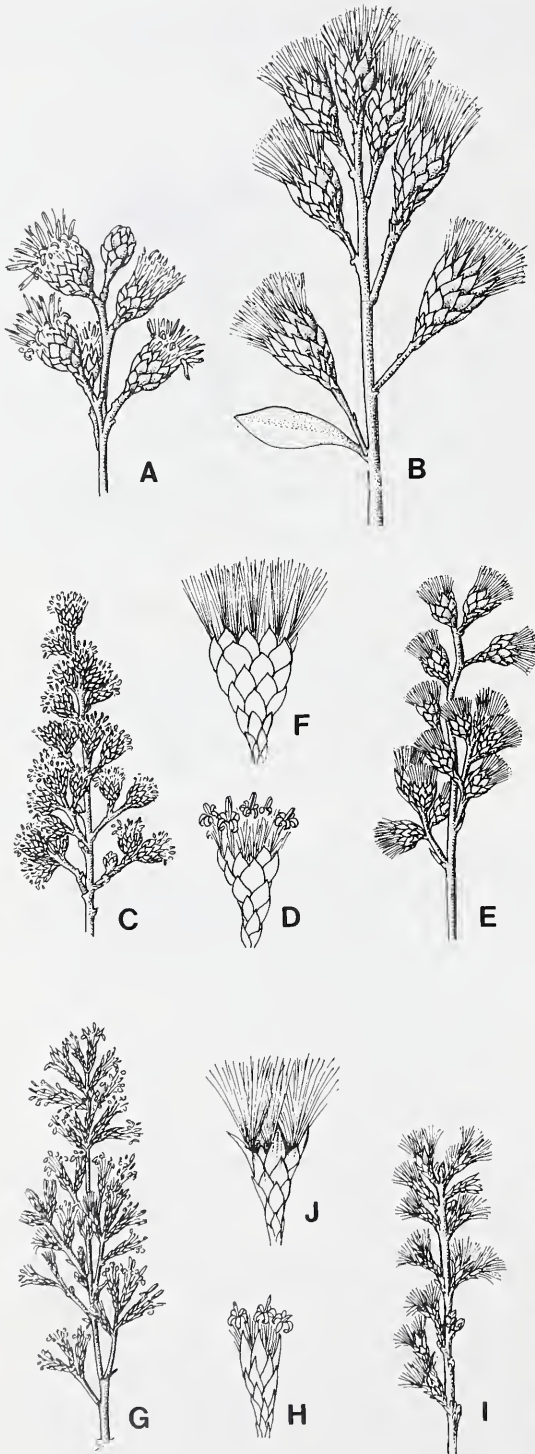


FIGURE 3.—Shape of involucre of ♂ and ♀ capitula of *Brachylaena* spp. A, B, *B. discolor*: A, ♂, × 1, Van Wyk 6120 & Mogg 38407; B, ♀, × 1, Strey 8789 & Schweickerdt 1384. C–F, *B. transvaalensis*: C, ♂, × 1; D, ♂, × 3, Galpin 451 & Van Vuuren 1278; E, ♀, × 1; F, ♀, × 3, O'Connor 1471 & Forester Evans 5398. G–J, *B. uniflora*: G, ♂, × 1; H, ♂, × 3, Kotze 432 & Medley Wood 12670, I, ♀, × 1; J, ♀, × 3, Bayliss BR1B1499 & Boocock 26. Artist: Gillian Condy.

Fegen 2060 (1) PRE. Flanagan 860, 861 (1) PRE. Forbes 330 (1) NH. Forbes & Obermeyer 28 (1) NH, PRE. Forestry Dept., Pta. s.n. Tvl. Mus. 9703 (2) PRE.

Galpin 451, 12114, 13995 (2) PRE. Gerrard & McKen 1017 (1), 1866 (3) NH. Gerstner 3013 (3), 4892 (2), s.n. PRE43300 (3) PRE. Gibbs Russell 3879 (1) PRE. Giffen 254 (1) PRE. Goodman 304 (1) NU. Gordon 162 (3), 348 (1) NH. Gordon-Gray 596 (1) NU; 607 (3) NH; 1580 (3) NU. Grenfell 1105 (2) PRE. Guy & Jarman 2 (2) NU.

Hafström & Acocks 1529 (2) PRE. Hall-Martin 1867 (1) PRE. Halse s.n. (3) NU. Hanekom 2312 (2) PRE. Harrison 29 (1) PRE. Hemm 268 (male plant) (2) PRE. Hillary 392 (2) NU. Hilliard 5068, 5069 (3) NU. Hubbard 6103 (1) PRE.

N. Jacobsen 1810, 2963 (2) PRE. W. Jacobsen 5329 (2), 4712 (1) PRE. Jones 55 (2) PRE. Jordaen 87 (2) PRE.

Karsten s.n. PRE31786, PRE43311 (2) PRE. Keet 1130 (2) PRE. Kluge 173, 1070 (2) PRE. Kotze 89, 450 (1), 432 (3), 2835 (2) PRE. Krige 19 (2) PRE.

Lansdell 66 (1) NH, PRE; s.n. NH34283 (1) NH. Law 71 (2) NU. Lawn 643 (3) NH. Letty 222 (1) PRE.

Macleod 19 (2) NU. Marloth 4174 (1) PRE. Marriott s.n. (1) PRE. McCallum 1532 (2) PRE. McMurtry 2190 (1) PRE. Meyer 6144 (1) PRE. Mills 342 (3) PRE; 469 (1) NH, PRE. Mogg 33761 (3), 38407, 38443 (1) PRE. Moll 1816 (1) NU, PRE; 4501 (2) NH. Munro P.S. 2 (1), 35, 213 (2) PRE.

Nel 258 (2) PRE. Nicholas 1637 (1) NH, PRE. Nichols 424 (1) NH. Nicholson 808 (3) PRE. Nixon 24 (1) NU.

Obermeyer s.n. Tvl. Mus. 35830 (2) PRE. Obermeyer, Schweickerdt & Verdoorn 349 (2) PRE. O'Connor 1471, 3559 (2) PRE. Oranje 2 (2) PRE.

Pegel NDO 119 NH59807 (3) PRE. Pole Evans H15719 (2) PRE. A. Prior s.n. PRE30046 (1) PRE. J. Prior 103, 304 (2) PRE.

Rauh & Schlieben 9721 (2) PRE. Ross 2115, 2118 (1) NH, PRE; 2383, 2388 (1) PRE. Rudatis 653 (3), 1089 (1) PRE.

Scheepers 692 (2) PRE. Schlechter 2886 (1) PRE. Schonland 3304 (1) PRE. Schrire, Van Wyk & Abbott 1782 (3) NH. Schweickerdt 1367 (1) PRE; 1368 (2) NH, PRE; 1384 (1) NH, PRE. Sikhakhane 110 (1) NH. Sim 19260 (1) PRE. Smuts s.n. PRE43373 (1) PRE. Stephen 385 (1) PRE. Stephen & Van Graan 1266 (1) PRE. Stewart s.n. PRE61399 (2) PRE. Suelau 23 (1) PRE; 192 (1) NH, PRE. Story 1289 (1) PRE. Strey 6894, 7658, 8753, 8783, 8789, 8790, 8791, 8792, 8793, 8798, 9909 (1) PRE; 8822, 8858, 8859, 9907 (1) NH, PRE; 8779 (1) NH; 8795 (1) NU, PRE; 8788 (1) NH, NU, PRE; 8754, 8797 (2) PRE; 8751, 8752, 8787, 8805, 8819, 8841 (3) PRE; 8784, 8804, 8820, 8824, 10973 (3) NH, PRE; 8823 (3) NU, PRE. Strey & Huntley 4292 (1) NH, PRE. Stubbings 4B (3) PRE.

Taylor 206 (1) NU. Thode 2927, 2936 (3) PRE; A1518, A1532 (1) PRE. Thorncroft s.n. Tvl. Mus. 2773, Tvl. Mus. 11174 (2) PRE. Thorns

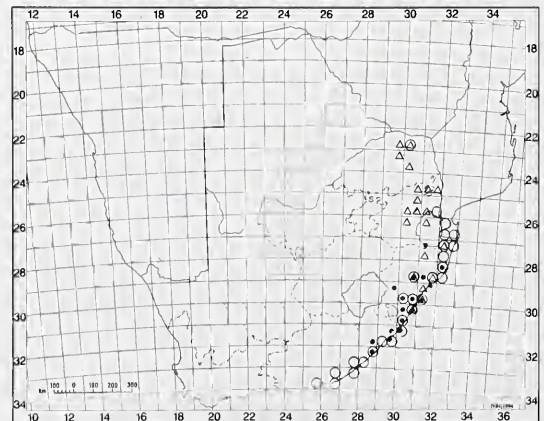


FIGURE 4.—Distribution of *B. discolor*, ○, *B. transvaalensis*, △, and *B. uniflora*, ●.



sub *Strey* 5785 (3) NU, PRE. *Tosh s.n.* NU30704 (1) NU. *Tustin* 3555, 3556 (2) PRE. *Tyson* 8575, 12571 (1) PRE.

*Van Jaarsveld* 748 (2) PRE. *Van Vuuren* 1278 (2) PRE. *Van Wyk* 6120 (1) PRE. *Van Wyk & Theron* 4600, 4741 (2) PRE. *F. Venter* 980 (3) PRE. *H.J.T. Venter* 1927 (1) PRE.

*C.J. Ward* 5810, 6624, 7137 (1) PRE; 2687, 6623, 7138 (1) NH, PRE: 22 (1) NU; 2630 (3) NH, PRE. *M.C. Ward* 25 (1) NU; 801 (1) NH, PRE; 504, 2090 (1) NH; 1542 (2) NH. *Wilcox* 1 (1) PRE. *Wirminghaus* 520 (1) NU. *Wood* 585 (3) NH; 4907 (1), 12287, 12670 (3), 12670a (1), 12670b (3) PRE. *Wright* 114 (1) PRE.

### Problem specimen

*Hemm* 268 (female plant, PRE), identified as *B. discolor*, is a very peculiar specimen totally out of the distribution range of the species and with smaller capitula than the usual *B. discolor*, but with stalked capitula and an involucre similar to that of *B. discolor*. Vegetatively it looks very similar to *Hemm* 268 (male plant, PRE), identified as *B. transvaalensis*.

### ACKNOWLEDGEMENTS

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## METZGERIALES–FOSSOMBRONACEAE

### FOSSOMBRONIA RWANDAENSIS, A NEW SPECIES FROM TROPICAL AFRICA

#### INTRODUCTION

In a previous paper (Perold 1997), reference was made to some specimens of *Fossombronia*, notably *De Sloover* 185.74, (BR, NAM) from Rwanda, which had been referred to *F. capensis* S.W.Arnell. The two taxa, *F. capensis* and the fertile Rwanda specimen placed here, have several characters in common: both are dioicous and have large perigonal bracts subtending the antheridia in the male plants and their elaters are similar in that they are poorly formed. The spore ornamentation in *F. capensis* and the Rwanda specimen is, however, completely different and in some capsules of the Rwanda species (particularly those held at BR) it even exhibits a degree of dimorphism. Since spore ornamentation is regarded as the most important character in distinguishing between species of *Fossombronia*, it must be assumed that we are here dealing with two different taxa. The records of *F. capensis* in tropical Africa (Vána *et al.* 1979; Wigginton & Grolle 1996) should therefore be deleted, as its distribution is seemingly restricted to a smallish area in the southern Cape winter rainfall region (Perold 1997); *F. rwandaensis* is described as a new species.

#### *Fossombronia rwandaensis* Perold, sp. nov.

Plantae prostratae, crebrae in coloniis. *Folia* imbricata, late patentia, irregulariter rectangularia. *Rhizoidea* purpurea. Dioicae. Plantae masculae communes; antheridiis bracteis magnis tectis, saepe binatim connatis. *Pseudoperianthium* late campanulatum, supra basin cra-

teriforme plicatum vel fimbriatum. *Sporae* 42.5–52.5 µm diametro, superficie distali plerumque cum cristis crassis, rarissime reticulata. *Elateres* 62.5–77.5 µm longi, debiliter formati. *Gametophyta* aliquantum similes sunt illis *F. capensis* (ut hae plantae olim agnotae sunt), sed sporarum ornamentis valde differunt.

TYPE.—Rwanda, préfecture de Gisenyi, sous le poste minier de Gikungu, alt. env. 2 000 m. Sur talus très humide, *J.L. De Sloover* 18.574 (NAM, holo.!, BR, iso.!).

Plants predominantly male, in dense overlying mats, green; shoots large, simple (Figure 6C) or once furcate (Figure 6A), rarely twice, up to 20 mm long, 1.8–2.0 mm high, 3.2–4.0 mm wide (up to 4.7 mm wide at pseudoperianth in female plants), apical segments moderately divergent, 2–8 mm long. *Stems* prostrate, sometimes tapering proximally, chlorophyllose, occasionally with a lateral bud, plano-convex in cross section, in male plants apically (Figure 5M) 200–250 µm (10 cell rows) high, 370–450 µm wide, basally (Figure 5N) 200–260 µm high, 280–350 µm wide, in female plants apically (Figure 5O), 250–330 µm high, 350–540 µm wide, basally (Figure 5P) 200–300 µm high, 350–450 µm wide. *Rhizoids* purple, 17.5–25.0 µm wide. *Leaves* overlapping, widely spreading, succubously inserted, irregularly rectangular longitudinally or transversely, upper margin and sometimes 'leading' edge ± rounded, with low protrusions here and there, 'trailing' edge occasionally sloping obliquely, with up to 6 unevenly spaced marginal slime papillae, ± 17.5 × 20.0 µm, sessile or raised on a basal cell; in male (Figure 5A–E) and

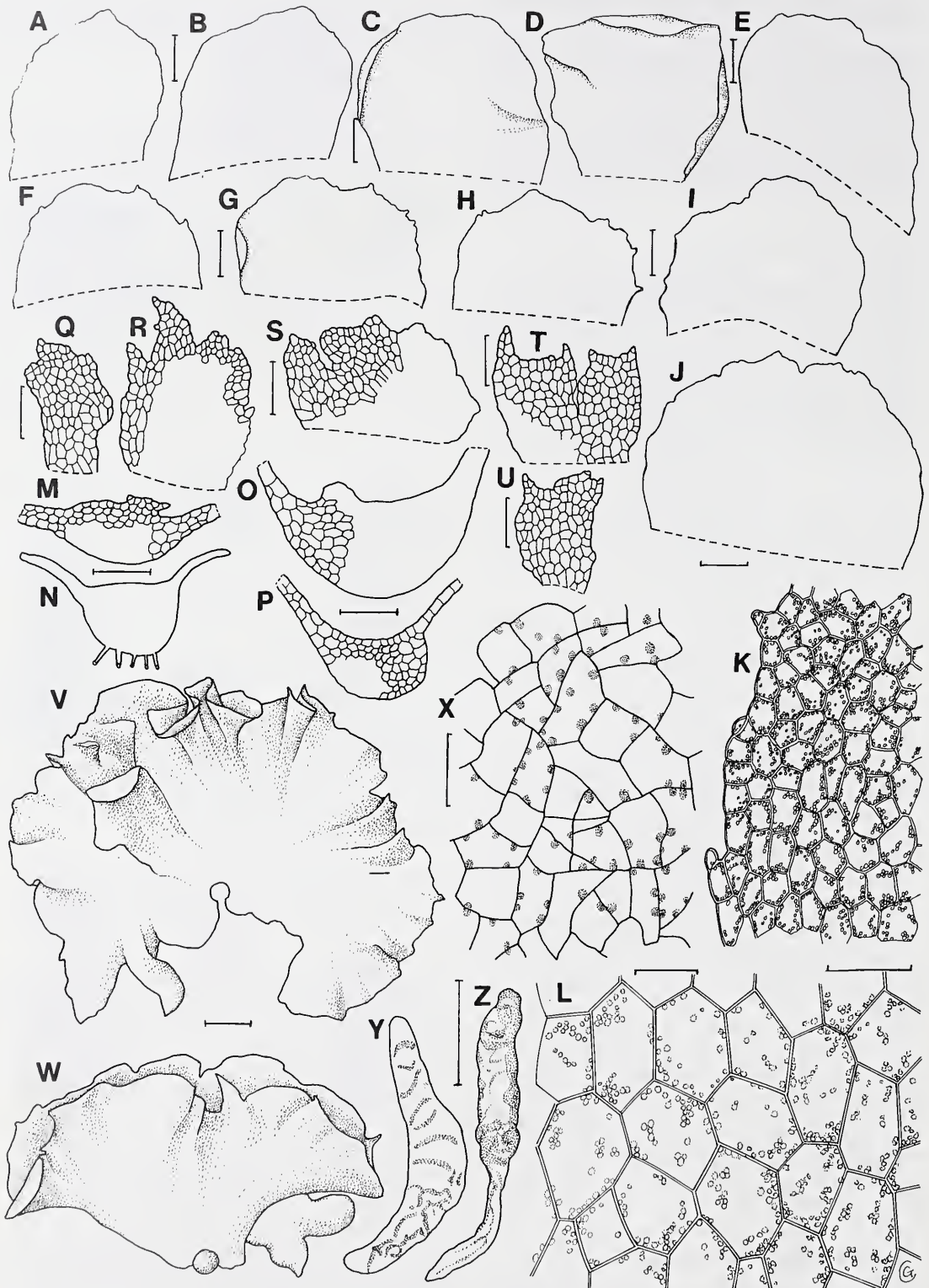


FIGURE 5.—*Fossombronia rwandaensis*, De Sloover 18.574. A–E, male leaves; F–J, female leaves; K, detail of trailing leaf margin; L, median leaf cells with chloroplasts (dotted lines), oil bodies no longer present in material studied; M, cross section of apical part of male stem; N, cross section of basal part of male stem; O, cross section of apical part of female stem; P, cross section of basal part of female stem; Q–U, perigonal bracts; V, opened pseudoperianth; W, pseudoperianth from side; X, cells in capsule wall; Y, Z, elaters. Scale bars: A–J, V, W, 500 µm; K, 100 µm; L, X, 50 µm; M–U, 250 µm; Y, Z, 25 µm. Drawn by G. Condy.



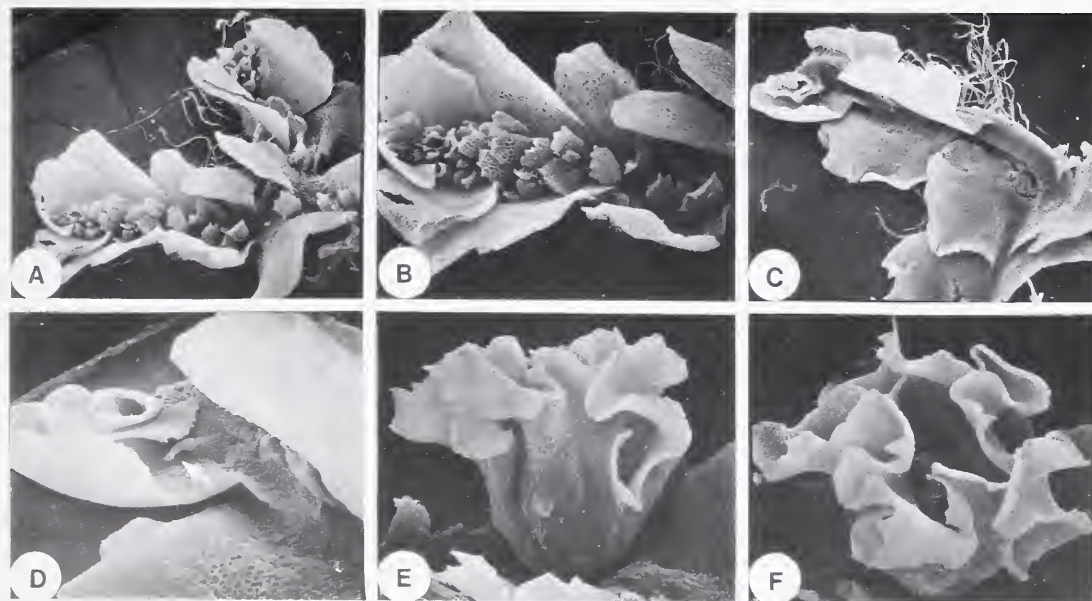


FIGURE 6.—*Fossombronia rwaendaensis*, De Sloover 18.574. A, moderately divergent terminal segments with rows of perigonial bracts subtending antheridia; B, detail of rows of perigonial bracts; C, apical part of female shoot; D, archegonium near apex (indicated by arrow); E, pseudoperianth from side; F, pseudoperianth from above. A,  $\times 14.4$ ; B,  $\times 24$ ; C,  $\times 12$ ; D,  $\times 33.6$ ; E,  $\times 22.8$ ; F,  $\times 23.4$ .

female plants (Figure 5F–J) not markedly different, (1075–)1500–2125  $\times$  1850–2250(–2900)  $\mu\text{m}$ , sometimes narrower above, up to 1625  $\mu\text{m}$  wide. *Leaf cells* thin-walled, at upper margins subquadrate to rectangular across, 17.5–32.5  $\times$  30.0–45.0  $\mu\text{m}$ , at lateral margins (Figure 5K), long-rectangular, 62.5–87.5  $\times$  32.5–42.5  $\mu\text{m}$ , upper laminal cells 5- or 6-sided, 45.0–57.5  $\times$  35.0–47.5  $\mu\text{m}$ , middle laminal cells 50.0–75.0  $\times$  40.0–50.0  $\mu\text{m}$ , basal cells 55.0–95.0  $\times$  50.0–67.5  $\mu\text{m}$ . *Oil bodies* lost in the material examined; chloroplasts clumped together at cell margins (Figure 5L),  $\pm 3 \mu\text{m}$  long.

Dioicous. *Antheridia* dorsal on stem, mostly in 2 crowded rows, short-stalked,  $\pm$  ovoid, 340  $\times$  300  $\mu\text{m}$ , shielded by perigonial bracts (Figure 6A, B), which are often in fused pairs (Figure 5R–T), 600–800  $\times$  550–600  $\mu\text{m}$ , when single (Figure 5Q, U),  $\pm 340 \mu\text{m}$  wide, margins with pointed or obtuse projections, up to 300  $\mu\text{m}$  long, marginal cells  $\pm$  rectangular or subquadrate, 25.0–42.5  $\times$  25.0–37.5  $\mu\text{m}$ , cells in interior 4- or 5-sided, 37.5–67.5  $\times$  30.0–40.0  $\mu\text{m}$ . *Archegonia* in 1 (Figure 6D) or 2 scattered rows along stem, naked; sometimes 2 in close proximity becoming fertilised. *Pseudoperianth* (Figures 5V, W; 6E, F)  $\pm 1.5 \text{ mm}$  proximal to apex, widely flaring and pleated or frilled above bowl-shaped base, about as tall as leaves, up to 2100  $\mu\text{m}$  long and 5500  $\mu\text{m}$  wide across mouth, at margin numerous projections, some rounded, others sharply pointed, with  $\pm 28$  slime papillae, mostly sessile, one-celled, 20  $\times$  20  $\mu\text{m}$ , a few raised on 3 tiers of basal cells, 42.5–50.0  $\times$  37.5–50.0  $\mu\text{m}$ , below with winged lateral outgrowths or appendages; cells not appreciably different in shape and size from those in leaves. *Capsules* globose,  $\pm 1000 \mu\text{m}$  diam., wall bistratose, inner layer (Figure 5X) rather pale, cells irregularly shaped, polygonal or roughly triangular to quadrangular, 37.5–62.5  $\times$  30.0–42.5  $\mu\text{m}$ , each cell wall with 2 or 3 brown, nodular thickenings, entirely lacking

semi-annular bands. *Seta* almost absent, as all capsules examined  $\pm$  sessile. *Spores* golden brown, with ridges, loops, blobs and very rarely reticulations deeper brown, hemispherical to occasionally somewhat irregularly shaped, a few still in tetrads (Figure 7H), 42.5–52.5  $\mu\text{m}$  diam., including spines projecting at periphery; distal face (Figure 7A–D) convex, with thick ridges, irregularly branching and curving or unbranched, short or long, straight or bent or looped, sometimes nodular, very rarely in some capsules only, reticulate (Figure 7G, I), with up to 13 small areolae across face; proximal face (Figure 7E, F) with triradiate mark rather indistinct to distinct, occasionally with nodules aligned along its arms, otherwise nodules scattered irregularly, size variable, up to 7.5  $\mu\text{m}$  wide, in between dusted with fine granules, around spore periphery 25–29 conical or truncate spines,  $\pm 3 \mu\text{m}$  long, unconnected by a perispore. *Elaters* (Figure 5Y, Z) few, rather delicate and poorly formed, often adhering to a spore, 62.5–77.5  $\mu\text{m}$  long, 10  $\mu\text{m}$  wide throughout or 15  $\mu\text{m}$  wide centrally and tapering to 10  $\mu\text{m}$  wide tips, difficult to distinguish the spirals, but apparently 3-spiral.

*Fossombronia rwaendaensis* has been named for the country where the type and only specimen with spores, De Sloover 18.574, was collected at high altitude in very humid conditions. Some maps that were consulted, give the spelling of the 'préfecture' as Kisenyi, not Gisenyi. The other De Sloover collections that were determined as *F. capensis* by Vána, De Sloover 13.345, 19.118, 19.169 (the latter from neighbouring Burundi) lack spores and can, therefore, not be identified with certainty, even though 13.345 has large perigonial bracts in the male plants. *F. rwaendaensis* can be distinguished by its dioicity, by large bracts subtending the antheridia, usually in 2 crowded rows dorsally along the stems of the male plants, by the cells in the inner wall of the capsules lacking semi-annular bands, by the coarsely ridged spores and by poor-

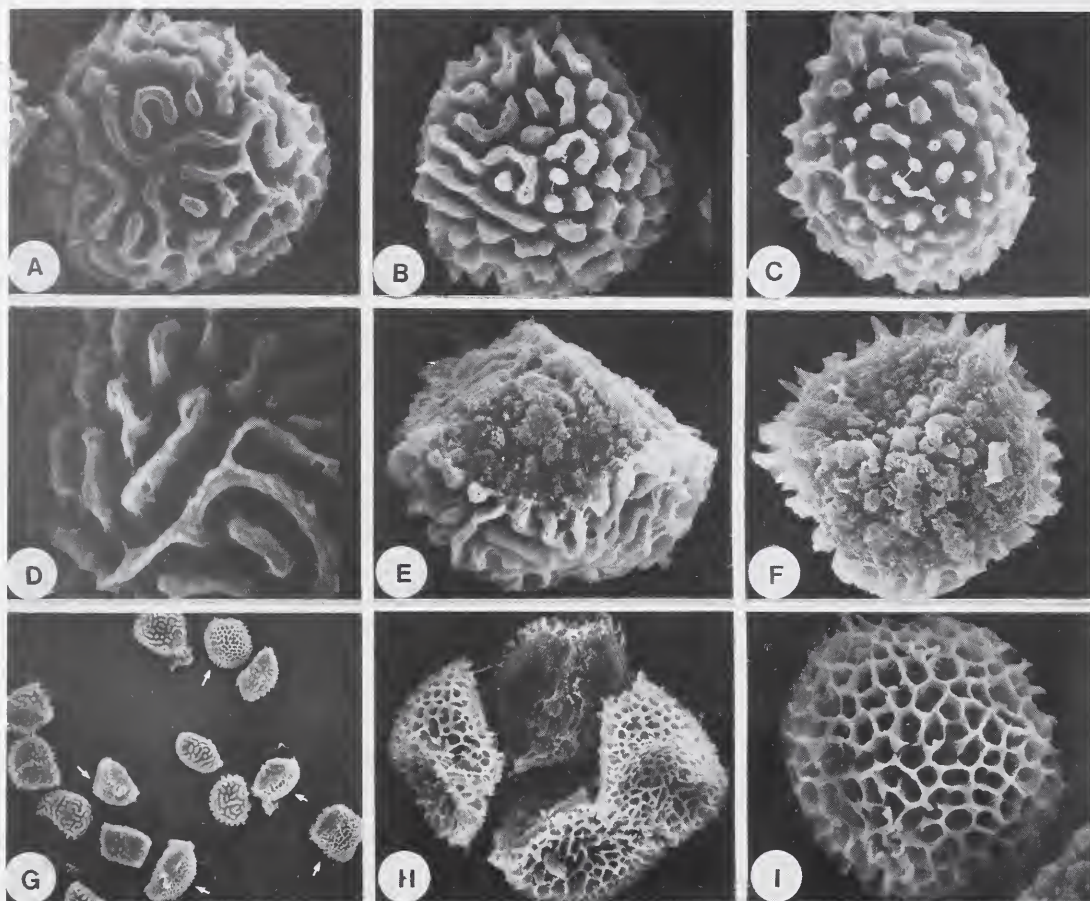


FIGURE 7.—*Fossombronia rwanadaensis*, De Sloover 18.574. Spores. A–C, distal face; D, detail of ridges near margin of spore; E, side view; F, proximal face; G, several spores in one field, some ridged, others reticulate; H, reticulate spores in partially broken tetrad; I, reticulate spore. A,  $\times 1200$ ; B,  $\times 995$ ; C,  $\times 1212$ ; D,  $\times 2160$ ; E,  $\times 1260$ ; F,  $\times 1030$ ; G,  $\times 190$ ; H,  $\times 545$ ; I,  $\times 1055$  (reticulate spores in G indicated by arrows).

ly formed elaters. As mentioned above, some capsules also contained a few spores that had reticulate ornamentation, either still in tetrads or already separated. Out of a total of 758 spores examined (from various samplings), only 24 or 3% had reticulate ornamentation, whereas all the rest, i.e. 97%, were ridged. The reticulate spores may be aberrant or still somewhat immature. As far as could be ascertained, they appeared to be absent from capsules that had been intact in the holotype specimen held at NAM. I think, however, that contamination of the capsules with occasionally reticulate spores, can be ruled out as a possible explanation for their presence. Paton (1973) observes that, 'Aberrant spores occur occasionally in this [i.e. *Fossombronia*] and other genera. Sometimes it appears that after the spore has attained full size, the development of the sculpturing has been arrested prior to final cutinisation. In such cases lamellae may be poorly developed or fragmentary'. Whether this would apply to the reticulate spores occasionally encountered in *F. rwanadaensis* remains a matter of conjecture.

*Fossombronia rwanadaensis* shares several characters with *F. capensis*, namely dioicity, large perigonal bracts and poorly formed elaters. The distribution of the latter is,

however, confined to a smallish area in the southern Cape winter rainfall region (Perold 1997). The lamellate spore ornamentation in *F. capensis* is also quite different. The records of *F. capensis* in tropical Africa (Vána *et al.* 1979; Wigginton & Grolle 1996) should, therefore, be deleted.

#### SPECIMENS EXAMINED

*De Sloover 13.345* (BR, NAM), Rwanda, forêt de Gishwati, le long de la route Gisenyi–Kibuye. *De Sloover 18.574* (NAM, holotype; BR, isotype), Rwanda, préfecture de Gisenyi, sous le poste minier de Gikungu, le long de la Bikoneko. *De Sloover 19.118* (BR, NAM), Rwanda, préfecture de Cyangugu, Forêt de Rugege, entre Gisakura et Karamba. *De Sloover 19.169* (BR), Burundi, au km 30 de la route Bujumbura–Ijenda, Matara.

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## THYMELAEACEAE

A NEW SPECIES OF *LACHNAEA* ENDEMIC TO THE SOUTHEASTERN MOUNTAINS OF THE WESTERN CAPE

***Lachnaea sociorum* Beyers, sp. nov., structura inflorescentiae florisque *L. ericoidis* similis, sed sepalis tomentosis, stigmatibus penicellatis, foliis lanceolatis ad angustum ellipticis, abaxiale leviter 3-costatis, apice acuto, glabris.**

TYPE.—Western Cape, 3321 (Ladismith): Langeberg, Bergfontein, S-facing midslopes of Koksposberg, 379 m, (–DC), 18-01-1991, McDonald 2059 (NBG, holo.; BOL, K. NY, PRE. iso.).

Erect, compact, moderately branched shrub up to 0.6 m tall, multistemmed at base, resprouting after fire. Branches erect, slender, ridged below leaf bases, covered with long, straight, adpressed hairs admixed with crooked ones, densely leafy, becoming naked with prominent leaf scars. Leaves alternate, ascending or occasionally inclined to patent, with apex curled inward, imbricate, sessile, lanceolate to narrowly elliptic or occasionally elliptic to obovate, 3.6–6.0 × 0.9–2.4 mm, coriaceous, green, those below inflorescence sometimes tinged maroon, glabrous, adaxially concave. Smooth, dull, ± white-punctate, abaxially convex, faintly 3-ribbed or subkeeled towards apex, glossy, subpapillate, apex acute, base cuneate. Inflorescence a terminal, sessile, ebracteate, 6–14-flowered umbel with up to 9 open flowers at a time, on main flowering branches. Flowers subactinomorphic, white, skunk-scented. Pedicel 0.3–0.7 mm long, sericeous. Hypanthium 2.5–3.7 mm long, circumscissile, three-fifths to three-quarters from base, upper portion funnel-shaped, tomentose outside, adpressed hirsute within, basal portion oblong, glabrous, rarely tomentose outside, glabrous within. Sepals 4, patent, subequal, widely ovate or subrotund, 1.7–3.0 × 1.7–3.2 mm, apex rounded or obtuse, adaxially and abaxially tomentose. Petals absent. Stamens 4 + 4, exserted, outer, antisepalous whorl inserted at base of sepals, 0.7–1.5 mm long, inner, antipetalous whorl inserted at rim of hypanthium, 0.5–1.2 mm long (inner stamens the shortest or equal to the shortest of outer stamens); anthers widely ellipsoid, 0.4–0.6 mm long, abaxially without broad connective tissue. Scales 8, exserted, inserted at mouth of hypanthium immediately below antipetalous stamens, obovoid or subglobose, 0.3–0.5 mm long, glabrous, translucent-white when fresh. Ovary ellipsoid or obovoid, 0.9–1.4 mm long, glabrous. Style linear-obconical, 2.0–2.9 mm long, with straight, adpressed or incurled hairs in upper half to two-thirds. Stigma penicillate. Chromosome number: 2n = 18 (Beyers 176). Figure 8.

## Leaf anatomy

Blade dorsiventral, epistomatic, glabrous, in transverse section slightly concave to more or less plane adaxially, convex abaxially (Figure 9). Cuticle well developed, thicker abaxially, surfaces papillate, with flaky wax deposits, particularly adaxially (Figure 10). Epidermis uniseriate, adaxial epidermal cells much smaller than abaxial ones, usually periclinally elongated; abaxial epidermal cells square to radially elongated, with outer tangential walls thicker than inner tangential walls (before gelatinisation), inner tangential cell walls of some cells gelatinised; adaxial epidermal cells incompletely and weakly gelatinised; stomata sunk below adjacent epidermal cells. Mesophyll differentiated into palisade and spongy parenchyma; palisade abaxial, 1- or 2-seriate; spongy parenchyma adaxial, cells palisade-like, loosely arranged with fairly large intercellular spaces. Vascular bundles comprising a large mid-bundle, flanked by 2 smaller lateral bundles on either side, with small intermediate bundles in between these two types; each bundle capped abaxially by large extraxylary fibres which are particularly well developed in the mid- and lateral bundles; bundle sheath present, uniseriate, parenchymatous, incomplete, interrupted by extraxylary fibre cap. Crystals of diosmin (potassium hydroxide test: Jackson & Snowdon 1990) present in adaxial epidermis and mesophyll, occurring as shagreen-like to somewhat dendritic masses, pale yellow; crystals and tanniferous deposits mutually exclusive. Tanniferous deposits present in all abaxial, and in some adaxial epidermal cells.

Vouchers: Beyers 176; McDonald 2059.

## Pollen morphology

Pollen grains shed as monads, spheroidal, pantoporate, 39–41 µm diam. Tectum reticulate with triangular suprategate subunits, (crotonoid pattern *sensu* Erdtman 1966); suprategate subunits triangular in surface view, with either a single central spinule or with usually four spinules, lateral sides of subunits straight or emarginate, surface around spinules striate to granular-striate, with muri (ridges) cross-linked in subunits with lateral sides emarginate. Figure 11.

Vouchers: Beyers 176; Oliver 10524.

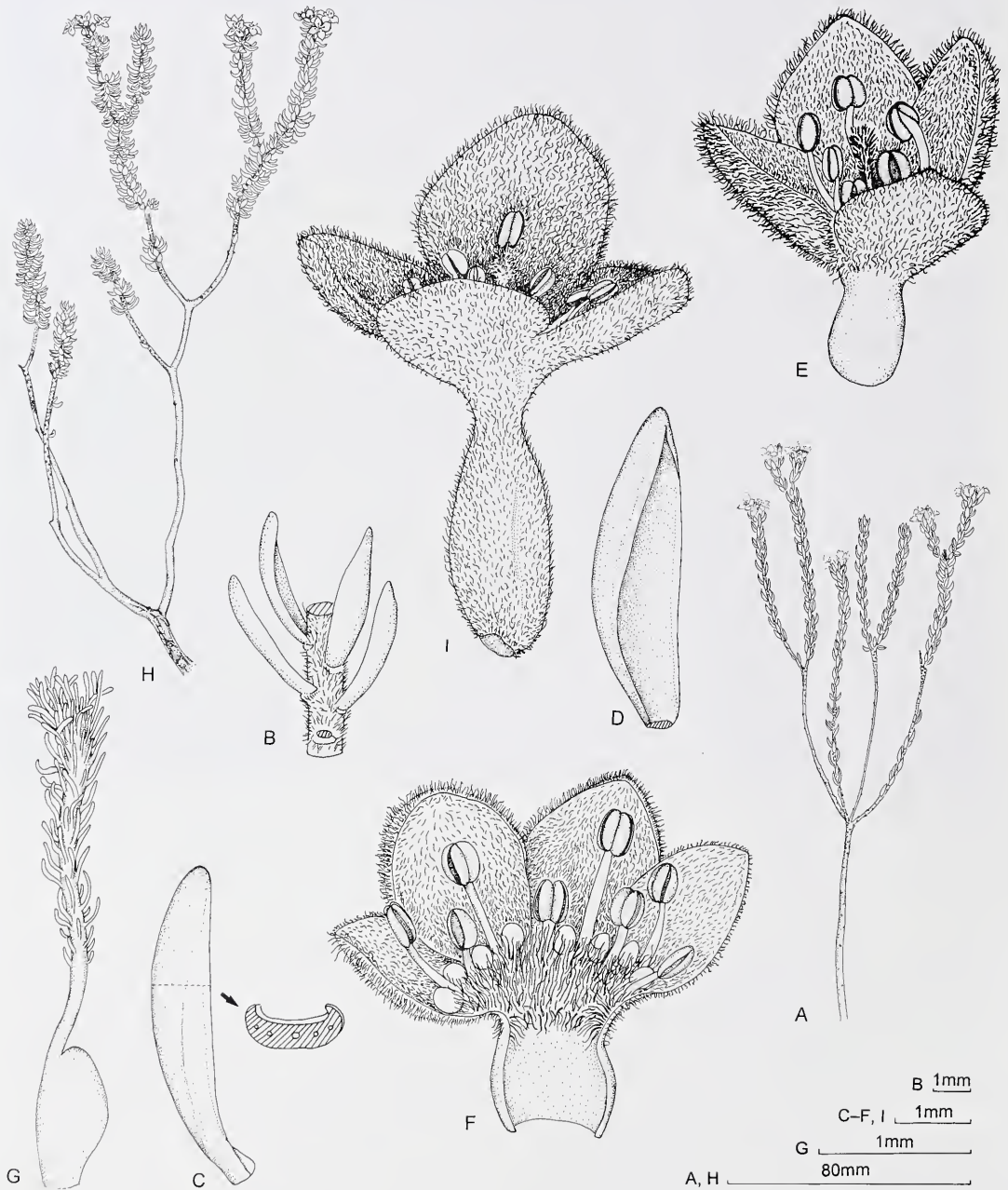


FIGURE 8.—*Lachnaea sociorum*. A, portion of plant; B, branchlet (enlarged); C, leaf (abaxial view and cross section); D, leaf (lateral view); E, flower; F, flower split longitudinally with gynoecium removed; G, gynoecium; H, portion of plant; I, flower; atypical pubescent form. A–G, McDonald 2059; H, I, Beyers 176.

#### Distribution, ecology and variation

Recorded from the eastern end of the Langeberg Mountains, from Perdeberg in the west eastwards to Gavelbos and the southern slopes of the Attakwa Mountains below Perdekop. Plants occur in stony soil on the southern and northern slopes, at altitudes between

300 and 1 100 m (Figure 12). Flowering recorded from August to January.

The population on the northern side of the Langeberg at Tygerberg, west of Huisrivier, is very localised and reasonably old. These plants are single-stemmed at the base, branching close to the ground and are open at the crown



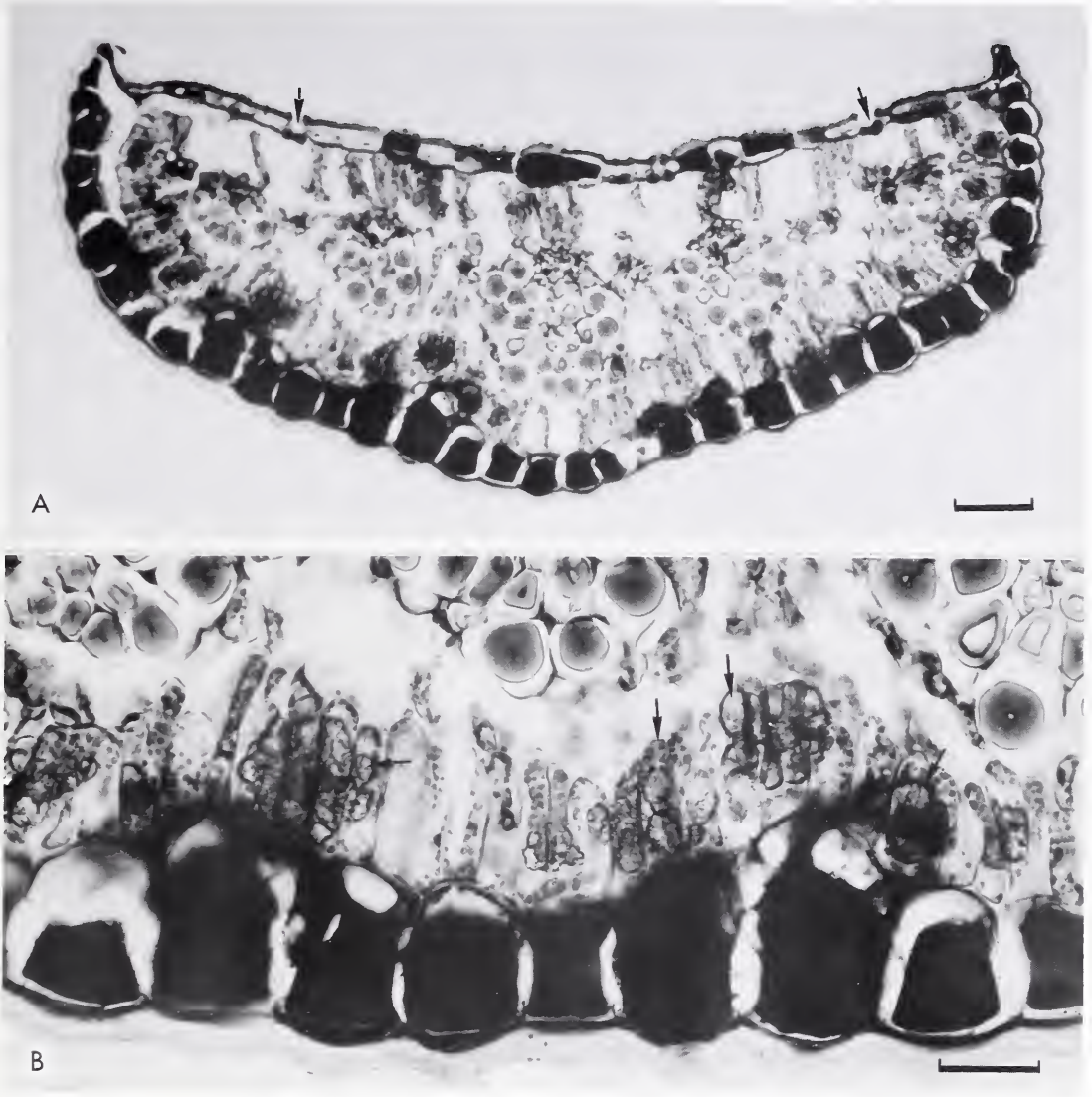


FIGURE 9.—*Lachnaea sociorum*, McDonald 2059, leaf anatomy, transverse sections. A, leaf lamina, note outline of shape, tanniferous epidermal cells (particularly abaxially), sunken stomata (arrowed) and vascular bundles with prominent caps of extraxylary fibres; B, portion of lamina showing tanniferous abaxial epidermal cells, adjacent palisade layer and extraxylary fibres, note masses of diosmin crystals (arrowed) in palisade cells. Scale bars: A, 100  $\mu$ m; B, 50  $\mu$ m.

with decumbent branches. Whether they would resprout after a fire remains to be seen. Two collections were made from this area, viz. *Beyers 176* and *McDonald 1780*. In all the material collected by McDonald, the basal portion of the hypanthium is glabrous as in all collections from other localities. However, in the material collected by Beyers the basal portion of the hypanthium on the outside is tomentose like the rest of the flower. This variation in hairiness needs further investigation before it can perhaps be formally expressed taxonomically.

#### Etymology

The specific epithet, *sociorum*, is derived from the Latin *socius*, meaning associate or colleague. This

species is dedicated to colleagues Ted Oliver and Dave McDonald, who on field trips always scouted for fresh *Lachnaea* material for the first author.

#### Diagnostic characters and relationships

*Lachnaea sociorum* is closely related to *L. ericoides* Meisn. Both have a similar inflorescence and floral structure. In both species the lower portion of the hypanthium is glabrous (except for the one collection of *L. sociorum*, *Beyers 176*, where it is tomentose). In *L. sociorum* the leaves are usually lanceolate to narrowly elliptic, abaxially faintly 3-ribbed, with an acute, glabrous apex, the sepals adaxially tomentose and the stigma penicillate. In *L. ericoides*, on the other hand, the leaves are narrowly

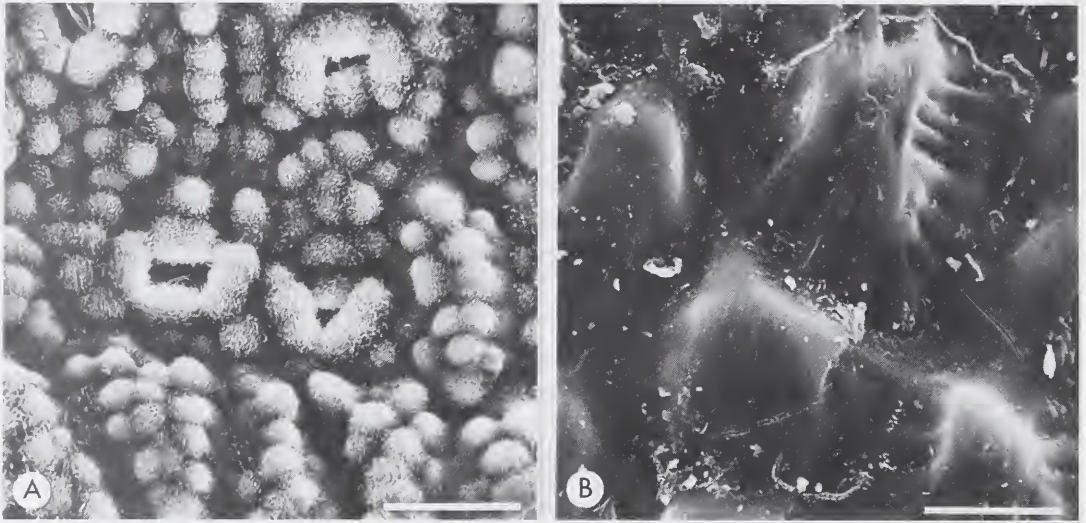


FIGURE 10—*Lachnaea sociorum*, McDonald 2059. SEM micrographs of leaf surfaces illustrating papillate cuticular relief. A, adaxial surface with dense flake-like wax deposit, B, abaxial surface with sparse flake-like wax deposit. Scale bar: 2 µm.

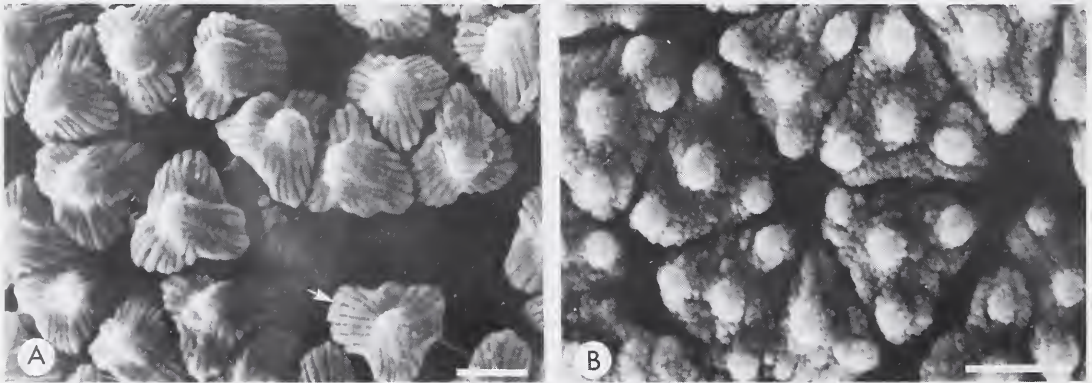


FIGURE 11—*Lachnaea sociorum*. SEM micrographs of acetolized pollen grains illustrating crotonoid tectum. A, supratectal subunits with single spinule, sides emarginate and with surface striate, note cross-links between muri (ridges), indicated by an arrow, McDonald 2059; B, supratectal subunits, each with usually four spinules, sides straight and surface granular-striate, Oliver 10524. Scale bar: 1 µm.

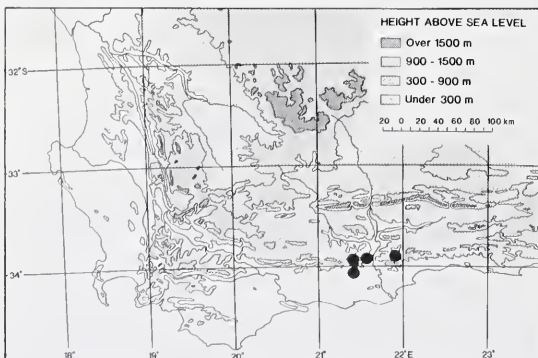


FIGURE 12.—Known distribution of *L. sociorum*.

elliptic to obovate, abaxially keeled, with a rounded, tufted apex, the sepals adaxially sericeous-tomentose and the stigma capitate with elongated papillae. The leaf anatomy of these two species is very similar except that in transverse section the leaves of *L. ericoides* are deeply concave adaxially and the extraxylary fibre strands capping the lateral vascular bundles are not as prominent as in *L. sociorum* (Beyers & Van der Walt 1995: fig. 8a).

#### *Specimens examined*

WESTERN CAPE.—3321 (Ladismith): Langeberg, Paardeberg, 1 100 m, (–CD), 11-08-1977, Haynes 1401 (NBG); E of Garcia's Pass on northern side of Langeberg, Tygerberg, west of Huisrivier, 300 m, (–DC), 15-12-1989, Beyers 176 (BOL, K, NBG, NY, PRE, Z), 17-12-1988, McDonald 1780 (BOL, NBG, PRE); Langeberg, Bergfontein area, lower slopes of Kokspesberg, 425 m, (–DC), 30-10-1990,



McDonald 1963 (PRE, NBG); Langeberg, Bergfontein, S-facing mid-slopes of Kokposberg, 379 m, (–DC), 18-01-1991, McDonald 2059 (BOL, K, NBG, NY, PRE); Riversdale Dist., Langeberg, W of Witselsberg, upper Witselsrivierkloof, 610 m, (–DC), 01-09-1994, Oliver 10524 (BOL, NBG, PRE); Langeberg, lower SW slopes of Witselsberg, N of Kokposberg, 488 m, (–DC), 01-09-1994, Oliver 10536 (BOL, K, NBG, PRE, Z); Mossel Bay Road to Perdekop before forest plantation, 600 m, (–DD), 17-10-1978, Bond 1578 (NBG), 3421 (Riversdale); Riversdale, Farm Gavelbos, mountain slope, SW aspect, stony soil, 307 m, (–AB), 08-09-1984, Bohmen 8479 (NBG, PRE). Grid ref. unknown: Riversdale Flower Show, 01-09-1994, comm. Oliver (NBG); Riversdale Div., Langeberg, 01-10-1923, Muir 2824 (BOL), Muir 3053 (PRE).

#### ACKNOWLEDGEMENTS

The authors would like to thank Mrs Inge Oliver for the line drawings, and Mr E.G.H. Oliver for translating the diagnosis into Latin.

### AYTONIACEAE (HEPATOPHYTA)

#### ASTERELLA ABYSSINICA NEWLY REPORTED FROM SOUTH AFRICA AND MALAWI

A specimen of *A. abyssinica*, Duckett & Matcham 6049, from Monk's Cowl, Drakensberg, Kwazulu-Natal, collected in April 1997, has recently come to hand by the generosity of Prof. J.G. Duckett, of the University of London. Besides this, I also collected this species in 1991 in Nyika National Park, Malawi (S.M. Perold 2664, 2672), from where it has not yet been recorded. The species is described and illustrated here. It is referred to the subgenus *Brachyblepharis* (Gottsche *et al.*) Grolle, because the short tips of the segments of the pseudoperianth separate at maturity. This is also the first report of the subgenus *Brachyblepharis* in both South Africa and Malawi.

*Asterella abyssinica* (Gottsche) Grolle in Vanden Berghen: 170 (1972).

*Fimbriaria abyssinica* Gottsche in Gottsche *et al.*: 569 (1846); *Hypenanthron abyssinicum* (Gottsche) Trevis.: 441 (1877); Steph.: 122 (1899). Type: Abyssinia cum *Targionia elongata*, in caespite Un. itin. n. 500 a Kotschy lecto pauca specimina inventa (not seen).

Thalli smallish to medium-sized, rather delicate and occasionally somewhat spongy, dorsally flat, green to light olive-green, crystalline when fresh, margins hyaline or tinged with mauve to deep purple, outlines of subdorsal air chambers faintly visible from above, medianly elongate and apically directed, laterally in radiating,  $\pm$  parallel rows, air pores not visible, encircling cells very slightly raised when wet; thallus margins flat or raised to partly inflexed when dry; in crowded, overlying mats, simple or once pseudodichotomously furcate (Figure 13A), with apical (often immediately distal to foot of stalk) or latero-ventral innovations from a tapering stipitate base. Branches ligulate to orbiculate, widening gradually from a narrow base, sometimes irregularly shaped and abruptly constricted, when simple, up to 15 mm long, when branched, total length  $\pm$  18 mm long, with terminal branches  $\pm$  5 mm long and moderately divergent, 2.3–5.0 mm wide, 400–450(–630)  $\mu$ m thick over midrib, laterally thinning out into attenuate wings, apex slightly notched, with appendages of few ventral scales recurved over

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edge; margins acute, thin, weakly scalloped, slightly undulate; ventrally the flanks of only the distal part purple, remainder green, but occasionally entirely purple, medianly keeled, midrib often green throughout, with row of purple scales on either side usually only distally present (Figure 13B), but sometimes along whole length.

*Dorsal epidermis* unistratose, containing chloroplasts, cells 5- or 6-sided when seen from above, thin-walled, (40.0–)45.0–65.0(–72.5)  $\times$  22.5–37.5  $\mu$ m, their orientation changing from apically directed medianly to outwardly sloping laterally, in transverse section 25.0–32.5  $\mu$ m thick (Figure 13E, F), toward margin occasionally containing an oil body; marginal cells (Figure 13H) mostly in 1(2) row(s), long- or short-rectangular, sometimes rather irregularly shaped, 22.5–30.0  $\times$  12.5–22.5  $\mu$ m; air pores hardly raised, simple, small,  $\pm$  12.5  $\times$  10.0  $\mu$ m, 80.0–137.5  $\mu$ m distant from each other, bounded by innermost circle of remains of collapsed cells (not shown), and outwardly surrounded by 2 intact, partly overlapping concentric rings of 6 or 7  $\pm$  wedge-shaped cells in each (Figure 13G), inner ones smaller, 10.0–15.0  $\times$  15.0–22.5  $\mu$ m, outer ones 15.0–20.0  $\times$  20.0–37.5  $\mu$ m; assimilation tissue 215–260  $\mu$ m thick, with small, empty air chambers (Figure 13E), 30.0–100.0  $\mu$ m wide, in 2 or 3 storeys, toward margins elongating and sloping obliquely, chlorophyllose cells in bounding walls rounded or elongated, 32.5–42.5  $\times$  27.5–30.0  $\mu$ m; storage tissue confined to keel,  $\pm$  220  $\mu$ m thick, cells angular, isodiametric, 17.5–27.5  $\mu$ m wide, closely packed together, occasional cells with an oil body; rhizoids arising from ventral epidermis of keel, smooth, 15.0–20.0  $\mu$ m wide, or pegged, 12.5–15.0  $\mu$ m wide. Scales in 2 forwardly directed ventral rows, one on either side of midrib (Figure 13B), in different shades of mauve to purple, obliquely triangular, with a single appendage (Figure 13I), body of scale up to 800  $\mu$ m long, 650–750  $\mu$ m wide at base, sometimes crescentic, cells 4–6 sided, 57.5–65.0  $\times$  27.5–40.0  $\mu$ m, with up to 11 smaller, colourless cells containing remains of oil body; appendage oblong to elliptical, 420–430  $\times$  300–310  $\mu$ m, sometimes constricted at base,  $\pm$  200  $\mu$ m wide, tapering above to a

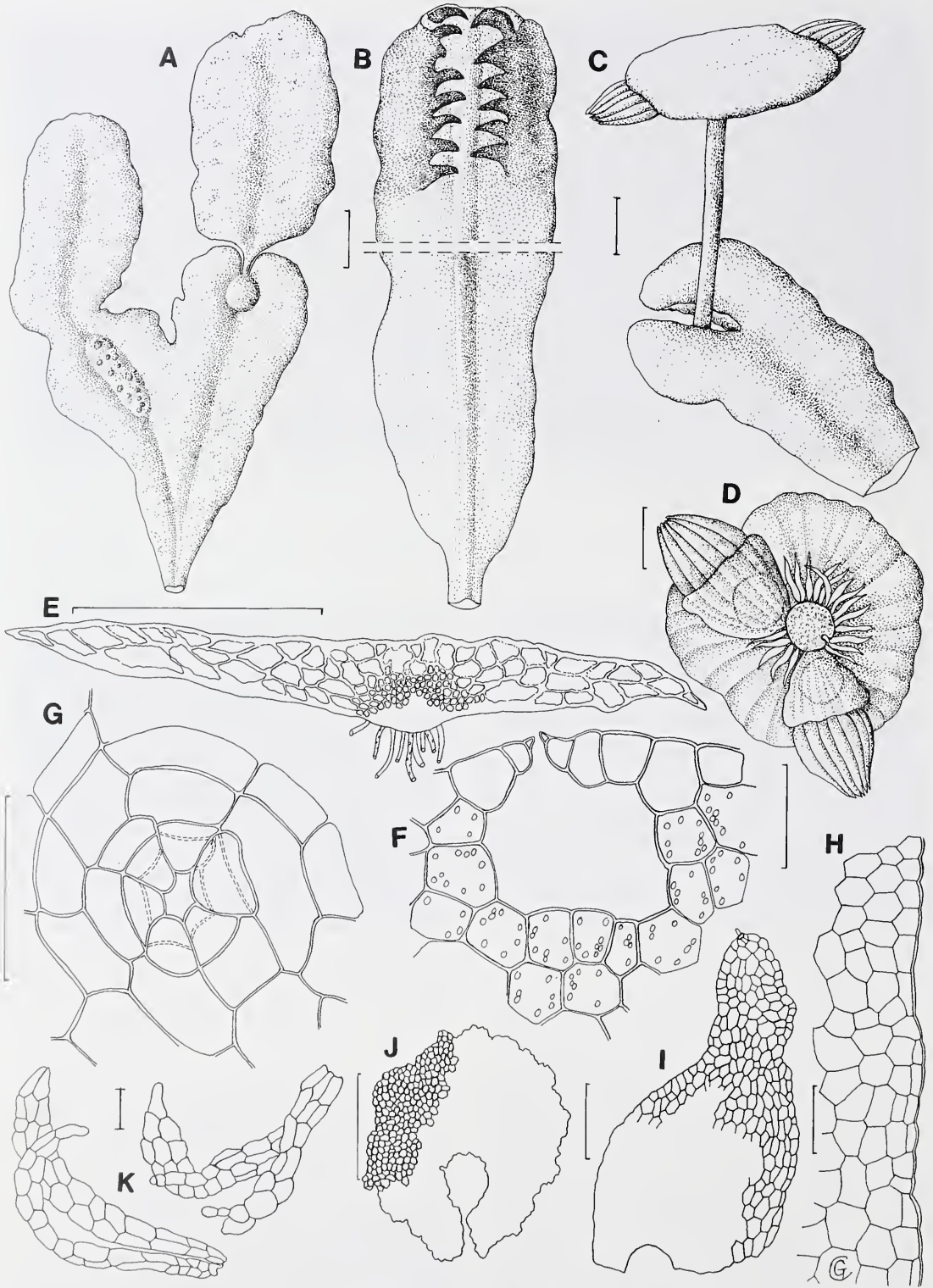


FIGURE 13.—*Asterella abyssinica*. A, dorsal view of branched thallus with gametoecia on separate branches of same plant; B, ventral view of thallus; C, carpocephalum raised on stalk; D, ventral view of carpocephalum; E, t/s of thallus; F, t/s of air pore and air chamber; G, air pore and surrounding cells from above; H, marginal cells of thallus; I, ventral scale; J, t/s of stalk; K, paleae. A–J, Duckett & Matcham 6049; K, S.M. Perold 2672. Scale bars: A–E, 1 mm; F–H, 50 µm; I, J, 250 µm; K, 100 µm. Artist: G. Condy.



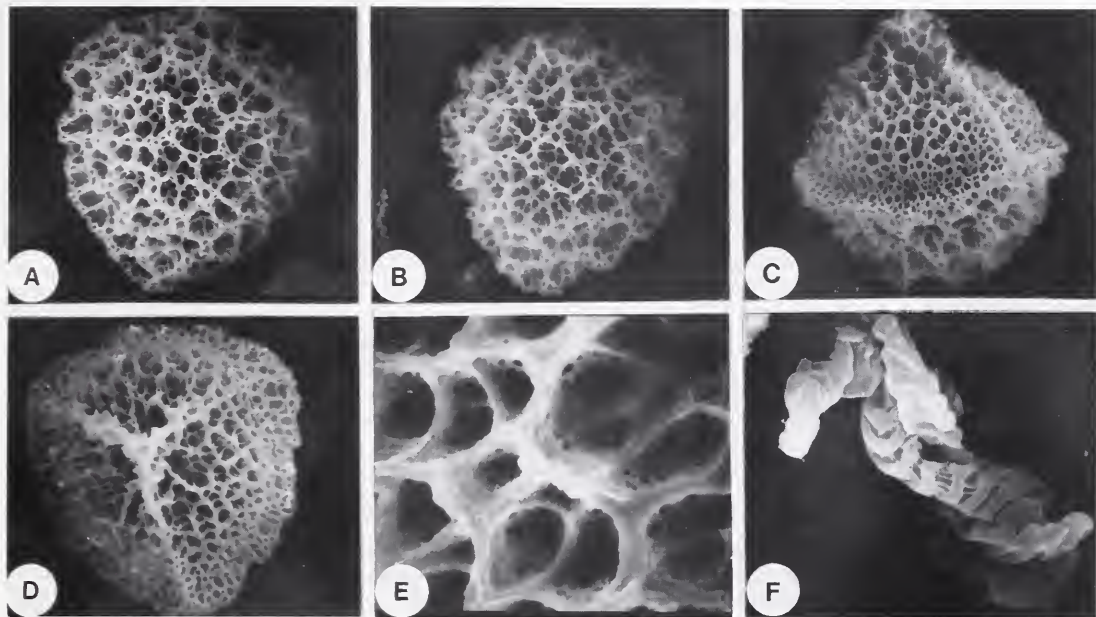


FIGURE 14.—SEM micrographs of *Asterella abyssinica*, Duckett & Matcham 6049. A–E, spore: A, B, distal face; C, side view; D, proximal face; E, much enlarged areolae on proximal face, basally highly porate. F, elater. A,  $\times 543$ ; B,  $\times 586$ ; C,  $\times 590$ ; D,  $\times 594$ ; E,  $\times 4104$ ; F,  $\times 679$ .

conical apical cell, marginal cells subquadrate,  $\pm 32.5 \times 35.0 \mu\text{m}$ , or rectangular,  $\pm 57.5 \times 27.5 \mu\text{m}$ , inner cells angular,  $32.5\text{--}50.0 \times 22.5\text{--}42.5 \mu\text{m}$ , only one cell containing an oil body,  $\pm 27.5 \times 25.0 \mu\text{m}$ ,

Autoicous, but androecia and archegoniophores sometimes on separate plants. *Androecia* extending backwards medianly, occasionally furcate, at apex of branch or more proximally at constriction (Figure 13A), antheridia immersed in sessile, elongated or oval cushions,  $\pm 1375 \times 750 \mu\text{m}$ , lacking scales and opening above via stout, raised, conical papillae,  $\pm 200 \mu\text{m}$  long. *Archegoniophores* proximal to apical notch of main branch (Figure 13C) or just proximal to stipitate innovation of apical branch (Figure 13A), single or occasionally paired at apices of 2 forking branches, almost sessile and hemispherical when young, paleae hidden (Figure 13A). *Carpoccephala* at maturity raised on stalk, arising  $\pm 1.7 \text{ mm}$  proximal to apex of branch in apical notch, length 4–5 mm, whitish green or streaked with purple, widening slightly toward base, in transverse section at midlength (Figure 13J),  $\pm 520 \times 450 \mu\text{m}$ , weakly ribbed, with a single rhizoid furrow containing pegged rhizoids, cortical cells not well differentiated, except for their outer walls being slightly thickened and rounded, variable in size,  $12.5\text{--}22.5 \times 12.5\text{--}15.0 \mu\text{m}$ , medullary cells angular,  $15.0\text{--}35.0 \times 15.0\text{--}27.5 \mu\text{m}$ ; scattered along length of stalk a few hyaline or purple paleae, 400–500  $\times$  160–180  $\mu\text{m}$ , at its summit numerous paleae (Figure 13K), hyaline or purple, up to 820  $\mu\text{m}$  long, basally 2 or 3 cells wide, above 3–5 cells wide,  $65.0\text{--}85.0 \times 35.0\text{--}47.5 \mu\text{m}$ , apical cell  $42.5\text{--}62.5 \times 17.5\text{--}22.5 \mu\text{m}$ ; disc green, rather flat to weakly convex, suborbicular (Figure 13C), 3.5–4.0 mm diam.,  $\pm 1.1 \text{ mm}$  thick, margin undulate, air chambers covered above by slightly bulging walls and opening via small, compound air pores, below (Figure 13D) with membranous, bistratose involucre

partly covering capsules like a flap, margin entire and unistratose, capsules mostly 2, rarely 1 or 3(4), obovate,  $1200 \times 950 \mu\text{m}$ , wall green, unistratose, cells elongated, 4- or 5-sided,  $45.0\text{--}75.0 \times 25.0\text{--}37.5 \mu\text{m}$ , thin-walled, toward apex of capsule rounded,  $35.0\text{--}47.5 \times 37.5\text{--}42.5 \mu\text{m}$ , walls with trigones at corners; pseudoperianths exerting horizontally from beneath rim of carpocephalum (Figure 13C) for  $\pm 1000 \mu\text{m}$ , colourless, split into 8–10 segments, these up to 1375  $\mu\text{m}$  long and 340  $\mu\text{m}$  wide at base, tapering to slender tips, which are initially attached, becoming free before capsule dehiscence. *Spores* 62.5–72.5  $\mu\text{m}$  diam., triangular-globular, pale yellow to yellow, translucent, wing undulate, up to 10  $\mu\text{m}$  wide, margin crenulate, distal face (Figure 14A, B) convex, reticulate, with network of  $\pm 6$  larger, primary areolae across,  $\pm 10\text{--}15 \mu\text{m}$  wide and extending over wing, their delimiting ridges only slightly raised and not clearly defined among the numerous criss-crossing walls of small, subsidiary areolae, areolar floor highly porate; proximal face with prominent triradiate ridge (Figure 14C, D), its arms continuous from pole to wing, but not clearly extending across, each of 3 facets with numerous areolae, larger at pole and smaller toward wing, but not clearly arranged in primary and subsidiary areolae, floor also highly porate (Figure 14E). *Elaters* yellow, 135–150  $\mu\text{m}$  long, 10  $\mu\text{m}$  wide in centre, slightly tapering to rounded ends,  $\pm 7.5 \mu\text{m}$  wide, with coiled, bispiral thickenings throughout (Figure 14F).

#### DISCUSSION

*Asterella abyssinica* is widespread in tropical Africa and has been reported by various authors from Burundi, Cameroun, Ethiopia, Rwanda, Sierra Leone, Tanzania, Zaïre and Zimbabwe (Wigginton *et al.* 1996). These are the first records, however, for South Africa (Figure 15) and Malawi. The species is generally found along stream-

Amended key to the southern African species of *Asterella* (see Perold 1994)

- 1a Pseudoperianth with segments apically free at maturity ..... subgenus *Brachylepharis* 1. *A. abyssinica*  
 1b Pseudoperianth with segments remaining apically attached at maturity ..... Subgenus *Phragmoblepharis*:
- 2a Thalli spongy, with tall air chambers mostly in one storey, and then not subdivided by supplementary partitions, each opening dorsally by a stellate pore; ventral scales occasionally fimbriate at single lanceolate appendage; carpocephalum round or umbonate and lacking paleae at summit of stalk; pseudoperianth extending  $\pm 300 \mu\text{m}$  beyond involucre and subdivided into 12 or 13 segments; spores  $75\text{--}95 \mu\text{m}$  diam., dark brown, ornamentation with irregular zig-zagging ridges ..... 2. *A. muscicola*
- 2b Thalli compact, firm, with small, low air chambers in several storeys, only some top ones opening above by a dorsal, non-stellate pore; ventral scales with 1 (or 2) lanceolate or ovate appendages, margin  $\pm$  entire; carpocephalum round or umbonate, papillose or  $\pm$  smooth, with paleae at summit of stalk; pseudoperianth extending more than  $1000 \mu\text{m}$  beyond involucre and subdivided into 14–16 segments; spores more than  $100 \mu\text{m}$  diam., yellow or brown, ornamentation with larger areolae generally containing subsidiary areolae:
- 3a Thalli smallish to large; carpocephalum covered with distinct papillae, projecting  $\pm 200 \mu\text{m}$ ; paleae at summit of stalk shaggy, dense, pale mauve or colourless, up to  $3000 \mu\text{m}$  long and 4 or 5 cells wide at base; ventral scales with lanceolate appendage; spores elaborately ornamented with 6–8 areolae across distal face,  $20\text{--}30 \mu\text{m}$  wide and ridges extending across wing, containing numerous subsidiary areolae (common, mostly summer rainfall species) ..... 3. *A. bachmannii*
- 3b Thalli medium-sized to very large; carpocephalum  $\pm$  smooth or with low papillae; paleae at summit of stalk colourless or purple, length variable; ventral scales with lanceolate or ovate appendages, spores less elaborately ornamented:
- 4a Thalli medium-sized; carpocephalum with umbonate head; paleae at summit of stalk mostly colourless, some very long, more than  $8000 \mu\text{m}$  in length,  $\pm 4$  cells wide at base; ventral scales with 1 or 2 lanceolate appendages; spores on distal face with (4–)6–9 areolae across,  $\pm 32 \mu\text{m}$  wide, very high ridges seldom extending across wing, usually containing small subsidiary areolae (winter rainfall species) ..... 4. *A. marginata*
- 4b Thalli large to very large; carpocephalum with rounded head, distinctly lobed below; paleae at summit of stalk almost colourless to purple,  $2000\text{--}3000 \mu\text{m}$  long, some up to 7 cells wide at base; ventral scales with single, large-celled, ovate appendage, constricted at base; spores on distal face with 5–8 areolae across,  $25\text{--}30 \mu\text{m}$  wide and extending to wing margin, almost empty of subsidiary areolae and hollow (summer rainfall, mostly Afromontane species) ..... 5. *A. wilmsii*

banks or on damp rocks. The thalli are rather thin and delicate and seemingly not adapted to drought conditions. The species can be recognised by the flattened discs of the carpocephala and by the horizontally protruding pseudoperianths, their rather short segments becoming free at the tips before the capsules dehisce.

## SPECIMENS EXAMINED

## South Africa

KWAZULU-NATAL.—2929 (Underberg): Drakensberg Park, Monks Cowl, near streambank on path to Crystal Falls, (–AB), 1 800 m, 21 April 1997, Duckett & Matcham 6049 (dupl. E, PRE), with *A. bachmannii* and *Turgionia hypophylla*.

## Malawi

NYIKA NATIONAL PARK.—1033: on path across river, leading to Juniper Forest, on soil of vertical bank, (–DB), 15 April 1991, S.M.

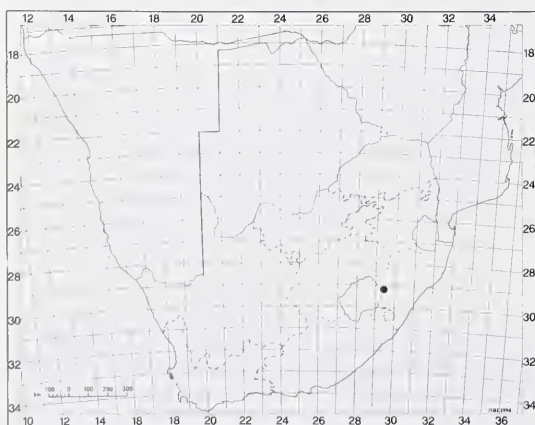


FIGURE 15.—Distribution of *Asterella abyssinica* in South Africa.

Perold 2664 (PRE); at bridge over Chelinda River, on rock and stone wall, (–DA), 16 April 1991, S.M. Perold 2672 (dupl. E, PRE).

## ACKNOWLEDGEMENTS

I sincerely thank Prof. J.G. Duckett for generously giving me a part of his and Matcham's collection of *Asterella abyssinica* from Monk's Cowl to deposit at PRE. Further thanks are due to Dr D.G. Long, for identifying my two Malawi specimens of *A. abyssinica* and for kindly refereeing this manuscript; also to the artist, Ms G. Condy, the typist, Ms D. Maree and the photographer, Mrs A. Romanowski, for their valued contributions.

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FABACEAE

A NEW SPECIES OF *PEARSONIA* FROM MPUMALANGA, SOUTH AFRICA

When the artist Anita Fabian was illustrating *Wild flowers of northern South Africa* (Fabian & Germishuizen 1997), she collected and illustrated a specimen of *Pearsonia* Dümmer from the Farm Paardekraal, near Dullstroom during 1991. The specimen was examined at the National Herbarium and was found to represent an undescribed species. For convenience, the caption of the illustration was left as *Pearsonia* sp. in Fabian & Germishuizen (1997). Subsequently more specimens of this taxon were found housed in the collections of PRE.

***Pearsonia hirsuta* Germish., sp. nov.** *P. aristatae* (Schinz) Dümmer similis sed habitu minore, foliis sessilibus ad subsessilibus, linearibus, dense pubescentibus, calycibus dense pubescentibus, area mediana alorum vexilligum pilis densis tecta, differt.

**TYPE.**—Mpumalanga, 2530 (Lydenburg): Dullstroom, Verlorenvallei Farm 95 JT, (–AC), 29-11-1980, *Drews 215* (PRE, holo.). Figure 16.

Small erect herb up to 150 mm tall, often resprouting from a perennial woody rootstock after burning in early spring; stems densely clothed with long, white to golden brown (especially on younger parts), appressed to spread-

ing hairs. *Leaves* exstipulate, sessile to subsessile; leaflets 3, linear to narrowly lanceolate, narrowed to an acute tip, densely white to golden brown, hairy on both surfaces, margin inrolled; mid-leaflet (6–)7–12(–16) mm long, up to 1 mm wide; lateral leaflets 5–8(–12) mm long, up to 1 mm wide (Figure 17A). *Racemes* lax, unbranched, few-flowered, terminal or mostly axillary on lower stems; pedicels up to 3 mm long; bracts ovate, 5–9 × up to 3 mm, persistent; bracteoles linear to narrowly lanceolate, 5–9 × up to 1 mm. *Flowers* yellow. *Calyx* 15–20(–22) mm long, densely covered with white appressed or spreading hairs; lateral lobes paired, narrowly triangular, up to 4 mm long; carinal lobe linear, up to 10 mm long; lateral sinus two to four times as deep as upper sinuses (Figure 17B). *Standard* elliptic to broadly ovate, 18–22 × 10–14 mm, lateral margins strongly reflexed, dorsal surface densely hairy in a broad median band from middle of lamina to apex outside, margin crinkled or crisped at apex (Figure 17C). *Wing petals* narrowly obovate, 15–20 × 3–5 mm; sculpturing present, upper middle comprising transcostal lamellae and densely bearded with white to golden brown appressed hairs. *Keel petals* small, narrow, 14–16 × 2 mm; shallow basal pockets present on outside, up to 0.5 mm deep. *Stamens* monadelphous; sheath 12–15 mm long, split adaxially to base; anthers 1.5 mm long, alternately basi-



FIGURE 16.—Holotype of *Pearsonia hirsuta* Germish.

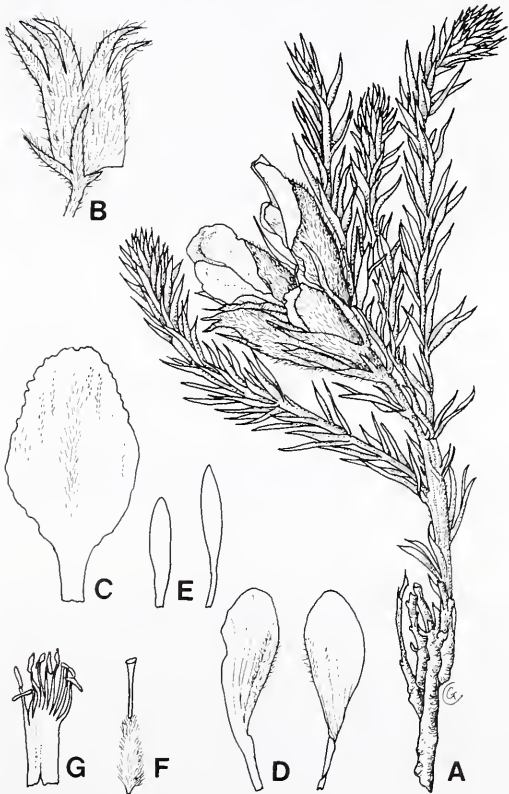


FIGURE 17.—*Pearsonia hirsuta*, *Drews 215*, holotype. A, flowering plant, × 1; B, calyx, × 1.5; C, standard, × 1.5; D, wing petals, × 1.5; E, keel petals, × 1.5; F, style, × 1.5; G, stamens, × 1.5. Drawing by G. Condy.

TABLE 2.—Differences between *Pearsonia hirsuta* and *P. aristata*

	<i>P. hirsuta</i>	<i>P. aristata</i>
habit	erect up to 150 mm	erect, spreading or prostrate up to 1.5 m
leaves	sessile or subsessile	distinctly stalked
leaflets	linear to narrowly lanceolate	ovate to elliptic

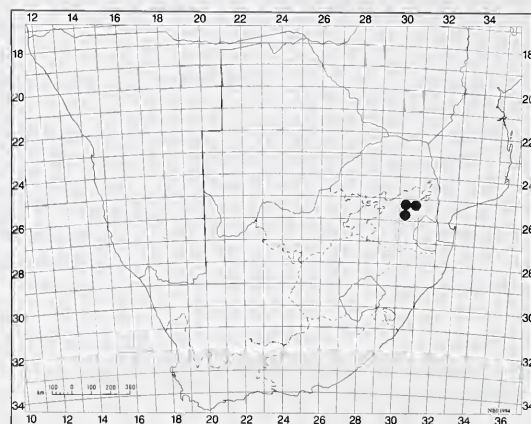
fixed and dorsifixed (Figure 17G). Ovary densely white-pilose, many-ovuled; style straight, glabrous; stigma capitate (Figure 17F). Fruit and seeds unknown.

Superficially *Pearsonia hirsuta* and *P. sessilifolia* (Harv.) Dümmer subsp. *filifolia* (Bolus) Polhill resemble one another. Polhill (1974), in his revision of the genus *Pearsonia*, describes the latter taxon as being a suffrutex with generally long, elongate, many-flowered racemes and the standard 8–13(–15) × 3.3–8.0 mm. *P. hirsuta* however, comprises short, few-flowered racemes and the standard is 18–22 × 10–14 mm. Differences between *P. hirsuta* and *P. aristata* are listed in Table 2.

*Pearsonia hirsuta* and *P. aristata* are allopatric. *P. hirsuta* occurs in the Lydenburg District of Mpumalanga (Figure 18), growing in low grassland between rocks in humus-rich sandy soil, whereas *P. aristata* occurs throughout the Northern Province, Mpumalanga, Swaziland, northern KwaZulu-Natal and into Zimbabwe. Flowering takes place during November. The specific epithet '*hirsuta*' refers to the hairy nature of this species.

#### Specimens examined

MPUMALANGA.—2530 (Lydenburg): lower foothills of Steenkampsberg, ± 34.5 km from Lydenburg on road to Roosenekal, (–AB), *Burgoyne 2046* (PRE); Dullstroom, Verlorenvallei Farm 95 JT, (–AC), *Drews 215* (PRE); Long Tom Pass, near cannon, (–BA),

FIGURE 18.—Distribution of *Pearsonia hirsuta* Germish. in South Africa.

*Burgoyne 2011* (PRE); Dullstroom District, crown of Farm Paardekraal, 'Oripi Falls', (–CA), *Fabian 1396* (PRE).

#### ACKNOWLEDGEMENTS

The author would like to thank Adela Romanowski for the photographs, Gill Condy for the drawing and Dr Otto Leistner for translating the diagnosis into Latin.

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## FABACEAE

### A NEW SPECIES OF *RHYNCHOSIA* FROM SOUTH AFRICA

The genus *Rhynchosia* is currently under revision. Herbarium and field studies have led to the discovery of an undescribed species which closely resembles *R. caribaea*.

***Rhynchosia atropurpurea* Germish., sp. nov.** *R. caribaeae* habitu similis sed foliis valde minoribus, stipulis maioribus, vexillo et alis valde brevioribus quam carina, et carina omnino atropurpurea. Figure 19.

TYPE.—North-West, 2527 (Rustenburg): Pilanesberg Game Reserve, near Saulspoort, (–AA), 5-1-1989, *Germishuizen 4977* (PRE, holo.).

A much-branched shrub, scrambling herb or perennial twiner up to 1 m tall; stems densely clothed with thin appressed soft hairs, especially on young parts, sometimes interspersed with patent, bulbous-based glandular hairs

and raised golden glands, becoming glabrous and shiny with age. Leaflets pinnately 3-foliolate; upper surface sparsely pubescent, with a few scattered glands, glabrescent; lower surface with prominent nervation, densely pubescent especially on margins and veins, with small raised golden glands scattered in intervinal areas; terminal leaflet 16–25(–33) × 16–22(–36) mm, broadly rhomboid or deltoid, gradually narrowed to an obtuse or subacute apex; lateral leaflets 15–22(–30) × 11–20(–22) mm, with lower margin distinctly gibbous; petiole 15–26 mm long; petiolules 5–12 mm long, canaliculate, stipellate (Figure 20A). Stipules up to 3.5 mm long, subulate, appressed, densely pubescent and glandular outside, glabrous inside. Inflorescences axillary, lax, unbranched, up to 13-flowered racemes; bracts up to 3 × 2 mm, ovate, reddish brown, pubescent, caducous; bracteolate. Flowers yellow with purple venation, keel deep purple to maroon. Calyx finely pubescent, glandular with raised golden glands and bul-



FIGURE 19.—Holotype of *Rhynchosia atropurpurea* Germish.

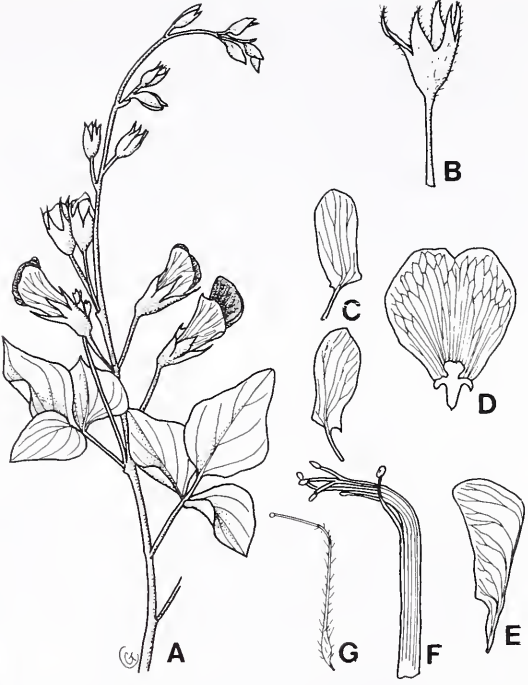


FIGURE 20.—*Rhynchosia atropurpurea*, G. Germishuizen 4977. A, flowering branch,  $\times 1$ . B–G,  $\times 1.5$ : B, calyx; C, wing petals; D, standard; E, keel petal; F, stamens; G, style. Drawing by G. Condy.

bushveld, to dense grassland with scattered trees on steep rocky granite hills. In contrast, *R. caribaea* occurs throughout southern Africa, except Lesotho. Flowering takes place from January to March, with fruiting concentrated in March and April.

The specific epithet '*atropurpurea*' refers to the characteristic dark purple keel of this species—in other species the purple marking is restricted to the apex of the keel.

*Specimens examined*

NORTHERN PROVINCE.—2327 (Ellisras): Mogol Nature Reserve, (–DD), Fourie 2588 (PRE). 2427 (Thabazimbi): Thabazimbi, western road, 5 km alongside road. (–CB), Nel 564 (PRU). 2430 (Pilgrims)

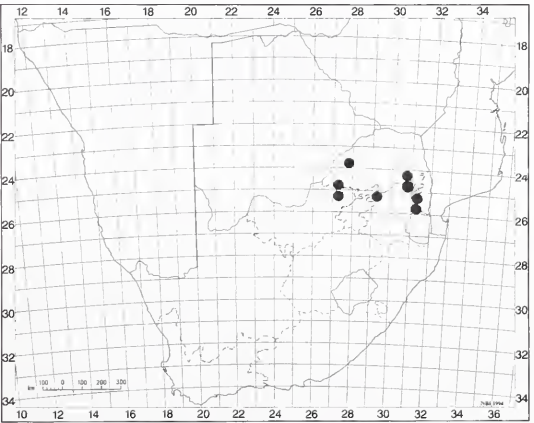


FIGURE 21.—The known distribution of *Rhynchosia atropurpurea* Germish.

bous-based hairs; tube 3.5–4.5 mm long; lobes narrowly triangular, carinal lobe up to 7 mm long, longer than other lobes (Figure 20B). *Standard* 15–16  $\times$  9–13 mm, broadly obovate to suborbicular, narrowing into an auriculate claw, sparsely sericeous with raised golden glands especially near apex on outside (Figure 20D). *Wing petals* up to 8 mm long, obovate to slightly cymbiform, slightly pouched (Figure 20C). *Keel petals* 17 mm long; pocket present on outside towards base, up to 1 mm deep; auricles present (Figure 20E). *Stamens* diadelphous; sheath split adaxially; anthers up to 1 mm long, alternately basifixed and dorsifixed (Figure 20F). *Gynoecium* up to 20 mm long; ovary 2-ovulate, densely white pilose; style bent in upper third, pubescent to point of flexure (Figure 20G). *Fruit* 35–44 mm long, oblong-falcate, narrowed towards base, recurving downwards at tip, conspicuously veined, covered with bulbous-based glandular hairs and raised golden glands. *Seeds* unknown.

Although *R. atropurpurea* and *R. caribaea* are superficially similar, *R. atropurpurea* differs from the latter in having much smaller leaves, larger stipules, the standard and wing petals much shorter than the keel petals and the keel dark purple to maroon throughout (in contrast to the yellow keel with maroon tip found in *R. caribaea*).

*Rhynchosia atropurpurea* occurs in the Northern Province, North-West and Mpumalanga (Figure 21), occupying a diverse range of habitats from ravine bush,



Rest): Abel Erasmus Pass, (–BC), *Van Wyk, Dahlgren & Kok* 5477 (PRE, PRU); beginning of Abel Erasmus Pass, (–BC), *Strey* 3281 (PRE); Hoedspruit Dist., Chester Farm, (–BD), *Burgoyne* 4090 (PRE);

NORTH-WEST.—2527 (Rustenburg): Pilanesberg Game Reserve, near Saulspoort, (–AA), *Germishuizen* 4977 (PRE).

MPUMALANGA.—2430 (Pilgrims Rest): foot of Kaspers Nek, on Ohrigstad road, (–DA), *Hilliard* 4722 (PRE); Mogaba California 228KT, (–DA), *Raal & Raal* 1743 (PRE). 2529 (Witbank): 5 km from Groblersdal on road to Marble Hall, (–AB), *Germishuizen* 3722 (PRE). 2531 (Komatipoort): Crocodile Valley Farm, 6 km from Nelspruit on Friedenau-Karino road, (–AC), *Coetzer* 823 (PRE, PRU); 15 km from Barberton on road to Kaapmuiden, (–CA), *Coetzer* 122 (PRE); Claremont Vale, 10 km north of Barberton, (–CA), *De Sousa* 229 (PRE).

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## ASPHODELACEAE: ALOOIDEAE

### *ASTROLOBA CORRUGATA*: DESCRIPTION OF A LONG-KNOWN SPECIES IN A SOUTHERN AFRICAN ENDEMIC ALOOID GENUS

Whilst compiling an account of the small southern African endemic genus *Astroloba* Uitewaal (Asphodelaceae: Alooideae) for Vol. 3 of the Synopsis Plantarum Succulentarum Project, co-ordinated by the Städtische Sukkulenten Sammlung in Zürich, Switzerland, it came to our attention that a well-known and frequently cultivated species of the genus has not been validly named.

The species is most commonly referred to as *Astroloba aspera* (Haw.) Uitewaal, but based on the original description of *Aloe aspera* provided in the protologue by Haworth (1804), this combination was established for a species of the genus *Haworthia* Duval. This is evident from the description of the leaf arrangement of *Aloe aspera* as '*foliis trifariis*' (Haworth 1804: 6). The leaves of species of *Astroloba* are arranged in five, not three, distinct rows, as the stems are viewed from above. This character has been adequately and unambiguously recorded as '*foliis quinquefariis*' in the description of e.g. *Aloe pentagona* (Aiton) Haw., which also appeared in Haworth (1804: 7).

If Haworth (1804) had given an adequate description of the flowers of the species, it could have given further clues to the exact identity of the novelty that he described as *Aloe aspera*. At the time, the flowers of species of *Haworthia* were usually simply described as '*in labio duo*', referring to the two-lipped flowers which are rather consistently encountered in *Haworthia* (see for example Haworth 1812: 90). Exceptions to this rule are representatives of *Haworthia* subg. *Robustipeduncularis* Uitewaal ex Bayer where the perianth somewhat resembles those of some species of *Astroloba*.

Eight years later, in 1812, the leaf arrangement of *Aloe aspera*, then clearly treated as a species of *Haworthia*, was again given as trifarious by Haworth. Furthermore, in his enumeration of the species he grouped his *Haworthia aspera* with the caulescent species of *Haworthia*, for example *H. viscosa*, and not with the other species nowadays included in *Astroloba*. The floral morphology was, however, clearly given as bilabiate, supporting the view that *Haworthia aspera* (Haw.) Haw. was in fact a species of *Haworthia* as generally circumscribed today. This name, *H. aspera*, was recently re-instated by Parr (1971), following his proposal to include *Astroloba* in *Haworthia*.

We do not uphold that interpretation.

Earlier, in 1811, Willdenow had the same view as Haworth (1812), although he included this species in the newly created genus *Apicra* Willd., a group which, in his concept, included all the species of *Haworthia* and *Astroloba*. The genus name *Apicra*, which was therefore an illegitimate renaming of *Haworthia* (Duval 1809), was unjustifiably taken up by Haworth in 1819 more or less solely for the species of *Astroloba*, as circumscribed today, and again the leaf arrangement of *Apicra aspera* (Haw.) Willd. was given as trifarious.

Salm-Reifferscheid-Dyck (1817), who preferred the Linnean concept of *Aloe* L. for all species currently dispersed amongst the genera *Aloe*, *Astroloba*, *Gasteria* Duval and *Haworthia*, accepted Haworth's (1804) interpretation of the trifariously leaved *Aloe aspera*. However, in 1840 Salm-Reifferscheid-Dyck extensively adapted the original description of Haworth by, amongst others, referring to the leaves of his *Aloe aspera* as '*foliis spiraliter quinquefariis*'. By so doing he essentially described a new species, but made the critical mistake of adopting Haworth's (1804) name, *Aloe aspera*. As argued above, this was undoubtedly a species of *Astroloba* and not *Haworthia*, since the flowers were unambiguously described as '*limbo regulari*'. The species as known today therefore does not have a legitimate name.

The final combination of the epithet *aspera* in the genus *Astroloba* was made by Uitewaal in 1947 (Smith *et al.* 1994; Smith & Van Wyk 1996). As basionym for this new combination he cited Haworth's (1804) concept of the species.

More recently two researchers working independently came to the same conclusion as us. Roberts Reinecke (1965), in an unpublished M.Sc. thesis proposed the name *Astroloba rugosa* for the species, whereas Groen (1987) proposed the name *A. muricata*. Neither of these names have been validly published and to prevent further confusion, we decided to choose the name *A. corrugata* N.L.Mey. & G.F.Sm. for this unnamed species.

A single variety, var. *major*, has been described in *Apicra aspera* by Haworth (1819). This variety was later

transferred to the genus *Astroloba*, as *Astroloba aspera* var. *major* (Haw.) Uitewaal (1947). In our opinion this entity does not warrant recognition at any rank, and should be included in the synonymy of *A. corrugata*.

In summary, the following names have been misapplied to this species: *Aloe aspera* Haw. (1804) and *sensu* Salm-Reifferscheid-Dyck (1817) not of Salm-Reifferscheid-Dyck (1840); *Apicra aspera* (Haw.) Willd. (1811); *Astroloba aspera* (Haw.) Uitewaal (1947); and *Haworthia aspera* (Haw.) Haw. (1812) and *sensu* Parr (1971). The names *Astroloba rugosa* Roberts Reinecke *ined.* (1965) and *Astroloba muricata* L.E.Groen *nom. prov. ined.* (1987) have been proposed for *Astroloba corrugata*, but were never formally published.

***Astroloba corrugata* N.L.Mey. & G.F.Sm., sp. nov.** ab aliis speciebus tuberculato-foliatis *Astrolobae* apicibus non-marginatus foliorum, distributione aequiore densioreque tuberculorum staturaque parviore foliorum differt.

**TYPE.**—Western Cape, 3320 (Montagu): Warmwaterberg, 7.5 km west of Warmwaterberg turnoff on Montagu–Ladismith road, (–BD), 27-02-1994, *E.J. van Jaarsveld 13913* (PRE, holo.).

Herbaceous, succulent perennial; caulescent, with leaves carried in  $\pm 5$  straight rows on vertical stem, up to 300–600 mm tall, 20–25 mm diam., solitary or proliferous from base and forming clusters. *Leaves* rigid, the young erect, the old spreading to more or less horizontal, 14–25 mm long, 11–18 mm broad at base, up to 5 mm thick, deltoid-ovate or lanceolate, sharply tapering, often twisted to one side in a spiral arrangement, tip pungent, light to dark green; upper surface flat to concave, tubercles concolorous, shiny, fairly evenly distributed, but tending to form raised longitudinal bands, up to 0.5 mm diam.; single distinct or indistinct keel occurring centrally or obliquely in distal third of leaf on upper surface, tubercled or with transverse ridges, keel not forming margin at apex; lower surface convex, similar to upper surface; margins upcurved, acute or rounded, rough. *Inflorescence* up to 430 mm long; peduncle simple, terete, 2–4 mm diam. at base, bracteate; sterile bracts membranous, ovate, acuminate, 4–8 mm long, erect, centrally keeled with reddish brown vein; raceme up to 270 mm long, lax, with 9–30 spirally arranged flowers and buds, 2–5 opening simultaneously; floral bracts membranous,  $\pm 5$  mm long, deltoid, acute, keeled with reddish brown vein, clasping pedicels, shorter than or as long as pedicels; pedicels erect, up to 9 mm long, up to 1 mm diam., green. *Flowers* subactinomorphic, funnel-shaped, white or cream with pink or greenish tinge, midribs of perianth segments green with beige or pink tinge; tube regular,  $\pm$  straight, slightly decurved apically,  $\pm 4$  mm across, constricted to 3 mm above; segments closely coherent, fused towards base; outer segments not adjacent, spoon-shaped, retuse at tips; tips flared,  $< 1$  mm long. *Stamens* 6 of two lengths, 5 and 6 mm long, inserted within perianth tube. *Ovary*  $4 \times 2$  mm, green; style 4 mm long, slightly curved, subcapitate, yellowish green. *Fruit* a trilobular capsule, cylindrical, apically retuse,  $\pm 12 \times 5$  mm diam. *Seed* dark grey, angled, shortly winged.



FIGURE 22.—*Astroloba corrugata*. Artist: Marietjie Steyn.

*Chromosome number:*  $2n = 14$  (Ferguson 1926; Majumdar 1968; Snoad 1951).

#### Diagnostic characters

*Astroloba corrugata* differs from the other tuberculate-leaved species, although glabrous members have been observed, in the genus by the non-marginate leaf

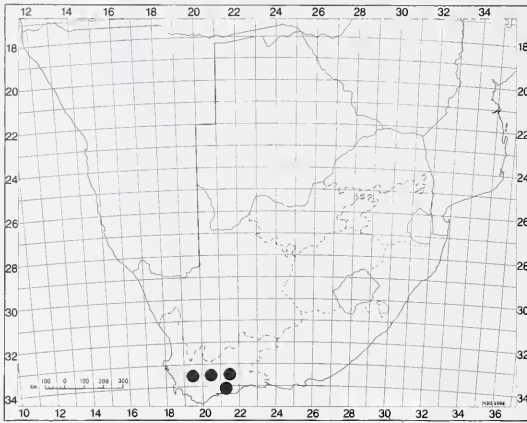


FIGURE 23.—Known geographical distribution of *Astroloba corrugata*.

tips and a more even, denser distribution of tubercles, as well as smaller leaf size. Furthermore, the affinities of *A. corrugata* would seem to lie with those species of the genus that lack a marked inflation of the perianth tube, viz. *A. bullulata* (Jacq.) Uitewaal, *A. congesta* (Salm-Dyck) Uitewaal and *A. foliolosa* (Haw.) Uitewaal. Only two smooth-leaved species, *A. herrei* Uitewaal and *A. spiralis* (L.) Uitewaal show this trait.

#### Etymology

The epithet *corrugata* refers to the wrinkled appearance of the leaves, imparted by the thickly dispersed, rough tubercles (Figure 22).

#### Distribution

*Astroloba corrugata* is widely distributed in the Ladismith, Montagu, Riversdale, Swellendam and Worcester Districts of the Western Cape Province of South Africa (Figure 23).

#### Conservation status

*Astroloba corrugata* is not threatened in any way (Hilton-Taylor & Smith 1994; Hilton-Taylor 1996).

#### ACKNOWLEDGEMENTS

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## HYACINTHACEAE

### A NEW SPECIES OF *ORNITHOGALUM* FROM THE RICHTERSVELD, SOUTH AFRICA

#### INTRODUCTION

Obermeyer (1978) recognised 54 species of *Ornithogalum* L. from southern Africa of which about 15 species, including the newly described species, occur

within the Richtersveld. In a recent publication U. & D. Müller-Doblies (1996) have extended the number of recognised species to 123 of which about 30 are recorded as occurring in the Richtersveld. These plants survive in all evolutionary niches from the highest mountains to the



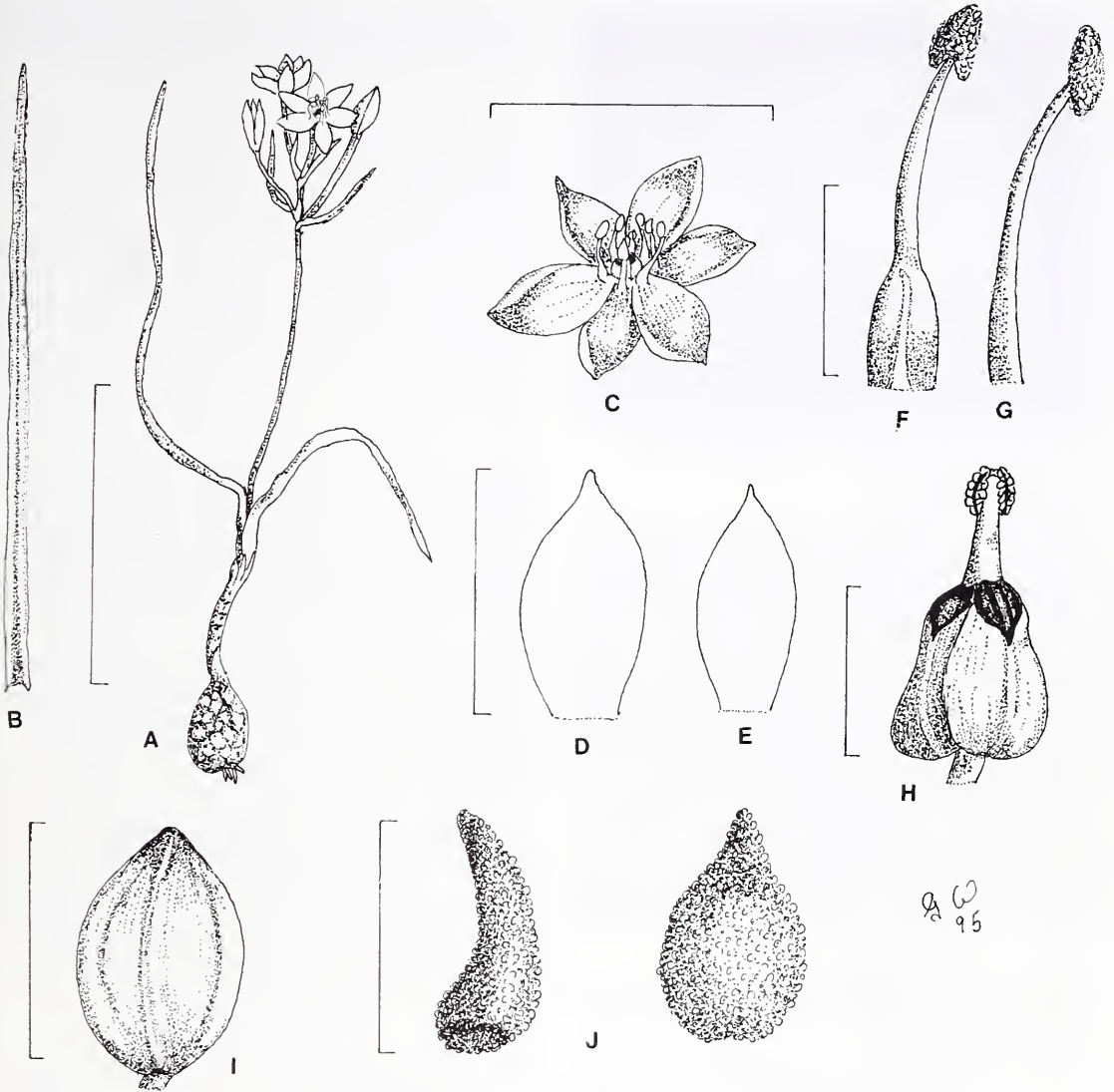


FIGURE 24.—*Ornithogalum decus-montium*, G. & F. Williamson 5803 (NBG). A, plant; B, leaf flattened (including basal sheathing portion); C, flower; D, inner and E, outer tepal; F, inner and G, outer stamen; H, ovary, style and stigma; I, capsule; J, seeds, side and front views. Scale bars: A, B, 45 mm; C, 16 mm; D, E, 7 mm; F, G, 2.25 mm; H, 2.5 mm; I, 4 mm; J, 1.5 mm. Drawn by G. Williamson.

low, more arid sandy plains. *O. decus-montium* appears to be restricted to the northern Richtersveld mountains.

***Ornithogalum decus-montium* G. Will., sp. nov.** ad subgenus *Aspasiam* et turmam *Aspasiae* pertinens. Species insignis apice ovarii nigrovirenti, a speciebus nobis notis bene distincta. *O. geniculatum* Oberm. primo adpectu simile, sed non-geniculato pedunculo satim diagnoscenda.

Planta bulbosa 40–100 mm alta (bulbo incluso); foliis 2, coetaneis, anguste linearibus, subacutis, 60–100 mm longis (vagina inclusa); scapo 60–100 mm alto, racemo ad 30 × 25 mm; seminibus commaformibus.

TYPE.—Northern Cape, 2816 (Oranjemund): Richtersveld National Park, ± 20 km E of Sendelingsdrift, (–BB), Sept. 1995, G. & F. Williamson 5803 (NBG, holo.).

Plant a dwarf geophyte 40–100(–120) mm high including bulb (Figure 24A). *Bulb* ovoid, 7 × 7 mm, outer tunic thin and brittle, pinkish brown with aerenchymatous layer ± 1 mm thick. *Leaves* 2, emerging from basal sheathing papyraceous cataphylls 3 mm long, synanthous, longest as long as scape, sheathing at base for 20–30 × 4 mm at widest, free portion light green, of soft texture, drooping to suberect, linear narrowing towards apex, subacute, 30–70 × 1.5–3.0 mm, glaucous with a smooth margin. *Scape* fine, wire-like, up to 100 mm; raceme up to 30 × 25 mm, 2–8-flowered, flowers subcorymbosely clustered and mostly facing skywards (Figures 24A, C; 25), bracts very narrowly linear, membranous, acute, 4–14 mm long; pedicels ± 10 mm long, suberect to erect, thin, wire-like, elongating up to 14 mm when capsule fully developed. *Tepals* shiny satin-white, outer narrowly elliptic, acute, 7 × 3 mm, inner elliptic, acute, 7 × 4 mm (Figure 24D, E). *Stamens*: filaments ±



FIGURE 25.—*Ornithogalum decus-montium*. Flower photographed east of Sendelingsdrift.

4.5 mm long, narrowing towards anthers, terete; inner with an oblong base; anthers rounded oblong, yellowish, all facing stigma, 0.8 mm long (Figure 24F, G). *Ovary* green, ovoid with apex very distinctly coloured luminous dark greenish black,  $2.5 \times 2.0$  mm; style terete,  $\pm 1$  mm long; stigma with 3 decurrent, papillate lobes,  $\pm 0.5$  mm long (Figure 24H). *Capsule* ellipsoid, green with longitudinal white stripes and darkened apex,  $4.0 \times 2.8$  mm wide (Figure 24I); seeds coal black, comma-shaped, densely tuberculate,  $1.5 \times 0.5$ – $0.8$  mm (Figure 24J).

*Flowering time:* in abundance in September.

*Etymology:* the specific epithet describes the scattered decorative carpets of flowering plants which cover the lower mountain slopes.

*Distribution:* The species is known only from the type locality and a second dense colony some 10 km to the west of this (Figure 26).

*Habitat:* open, exposed, undisturbed, arid mountain slopes at about 200 m altitude, in soils derived from sur-

rounding decomposing orange-brown igneous rocks. The main geological formation is the Vioolsdrif Suite. Plants only occur on the southwest aspect in full sun.

*O. decus-montium* falls into subgenus *Aspasia* group *Aspasiae* by possessing narrowly boat-shaped bracts with a smooth margin and as long as the pedicels, broad perianth segments with no dark rib and the style shorter than the ovary. It is synanthous with narrow leaves. The new species shows some similarities with *O. diphyllum* Baker but *O. diphyllum* has up to 3 leaves with inrolled margins and an inflorescence which usually has more flowers (up to 10), the perianth segments are more rounded-ovate and the stamens are usually longer (5 mm). Furthermore *O. decus-montium* has the unique feature of a luminous greenish black ovary apex. *O. diphyllum* is restricted to the Drakensberg range in the summer rainfall region of southern Africa, whereas the new species is endemic to the arid mountains of the northern Richtersveld just south of the Orange River. This area receives about 25–50 mm winter precipitation per year. Rainfall figures were obtained from the nearby Rosh Pinah Mine in Namibia and from the recently established weather station at Sendelingsdrift. The lower Orange River valley and adjacent mountains are bathed by sea fogs (mainly in winter) moving up the river in a north-easterly direction. The fogs tend to dissipate in the region of Lorelei where the river gorges wind towards the south-east. The new species occurs in the area where the fogs almost cease to have any marked effect.

*O. decus-montium* shares some characters with *O. multifolium* Baker which also occurs in the Richtersveld, viz. narrow leaves, long flower bracts, broad perianth segments and the style shorter than the ovary. However *O. decus-montium* occurs in a completely different habitat niche, is synanthous not hysteranthous, always produces only two leaves (*O. multifolium* has up to 6 leaves) and the flowers are white as opposed to yellow.

The new taxon also bears a superficial resemblance to *O. geniculatum* Oberm. but is immediately separated from this species by the sharp-angled peduncle where it

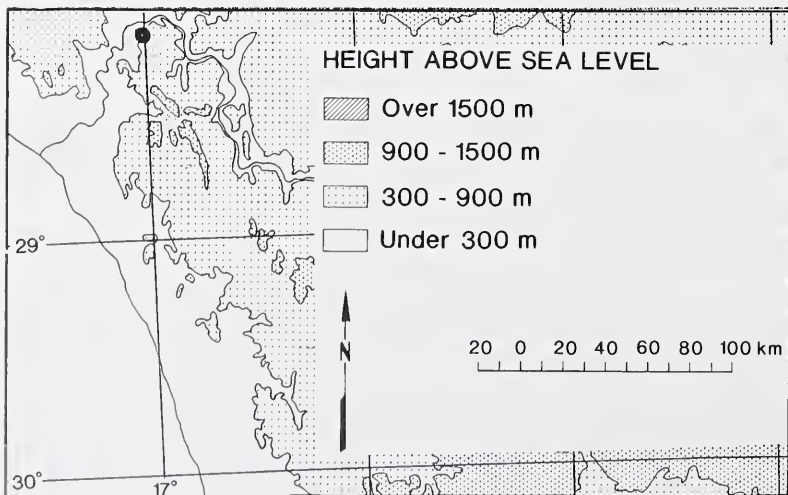


FIGURE 26.—Known distribution of *Ornithogalum decus-montium*.

emerges from the uppermost leaf. Furthermore *O. geniculatum* is found in the Richtersveld only under moist, fog dependent conditions in shady places.

Plants associated with *O. decus-montium* include several species which occur mainly in the arid eastern lower Orange River floristic zone, viz. *Tylecodon hallii*, *Schwantesia herrei*, *Conophytum loeschianum*, *Stoeberia carpii* and *Astridia hallii*. Arid associates which have distributions beyond the lower Orange River valley also occur nearby: *Pachypodium namaquanum*, *Euphorbia virosa*, *Sarcocaulon flavescens*, *Hoodia gordonii*, *H. alstonii*, *Crassula garibina*, the asclepiad *Pentarrhinum abyssinicum* subsp. *angolense* and the trees *Maerua schinzii* and *M. gilgii*.

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### OXALIDACEAE

#### TAXONOMIC DELIMITATION OF *OXALIS ENGLERIANA*

In the most recent revision of *Oxalis* L. in southern Africa, Salter (1944) regards *O. engleriana* Schltr. and *O. henrici* F.Bolus as two separate species in the section *Angustatae* subsection *Multifoliatae*. He does, however, mention that *O. henrici* was only known to him from the type specimen [Bolus 13079, Worcester Division; near De Doorns, (BOL)] and comments on its close morphological affinity with *O. engleriana*. The type specimen of *O. henrici* appears to be starved and the leaves are underdeveloped. Based on field observations, Bayer (pers. comm.) regards *O. engleriana* and *O. henrici* as conspecific. No constant interspecific morphological evidence could be found to justify their separate taxonomic status.

In a comprehensive palynological review of the southern African members of *Oxalis*, Dreyer (1996) found the pollen of these two species to be identical, but quite different to that of the rest of the genus. Both have reticulate grains with large, open luminae, prominent intraluminary bacules and very distinct supratectal spinules. Elsewhere in the genus, such unique deviations

from the basic reticulate pattern always occur in monotypic groups. Although palynological evidence alone is mostly not enough to substantiate taxonomic delimitations, we believe that in this instance it provides conclusive support to place *O. henrici* in synonymy under the older name *O. engleriana*.

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# New combinations in *Antimima* (Ruschioideae, Aizoaceae) from southern Africa

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**Keywords:** Aizoaceae, *Antimima*, new combinations, *Ruschia*, Ruschioideae, southern Africa

## ABSTRACT

As a consequence of the emended description of *Antimima* N.E.Br. by Dehn (1989) and based on extensive comparison of all types of the genera *Antimima* and *Ruschia* Schwantes, and on studies of about 250 fresh collections of *Antimima*, 95 species are transferred to that genus from *Ruschia*. The arguments for this step, and brief diagnoses of the 100 known species of *Antimima* are given. One species is excluded.

## INTRODUCTION

Brown (1930) described the genus *Antimima* with a single species, *A. dualis* (N.E.Br.) N.E.Br.—this species was first named *Mesembryanthemum duale* N.E.Br. (Brown 1920) and was transferred to the genus *Argyroderma* N.E.Br. (Brown 1922), based on similarities of leaf morphology and the light greyish white colouring of the leaves. When, after 18 years of cultivation of the plant, Brown saw a flower and realized that the species was not a member of the genus *Argyroderma* since it lacked the hypanthium characteristic of that genus (Figure 1 A, B).

The species had meanwhile also been described as *Ruschia dualis* L.Bolus (1929), but based on a different type. This name has been used for about 60 years, implying that the genus *Antimima* was a synonym of *Ruschia* Schwantes.

In the course of his studies in the Ruschiinae, Dehn (1989) found that not only *Antimima dualis* but also  $\pm$  100 species formerly in the genus *Ruschia* differed so markedly from typical forms of the latter genus, that he re-established the genus *Antimima*. He distinguished five subgenera and made four new combinations: *A. alborubra* (L.Bolus) Dehn, *A. longipes* (L.Bolus) Dehn, *A. microphylla* (Haw.) Dehn, and *A. virgata* (Haw.) Dehn. Later, *Antimima hantamensis* (Engl.) H.E.K. Hartmann & Stüber (1993) and *A. aurasensis* H.E.K. Hartmann (1996) were added.

In a comprehensive survey covering all species of the Aizoaceae, material of types of all species in *Ruschia* and fresh material of  $\pm$  250 collections of *Antimima* was examined. As a result, 95 species are here transferred to *Antimima*. With *A. virgata* transferred back to *Ruschia*, based on comparisons of fruits and the type, *Antimima* at present comprises 100 species.

The subdivision of the genus into subgenera will have to be dealt with on a much broader basis. M. Dehn (pers. comm. 1992) noticed that the circumscriptions of the

subgenera need reconsideration, in the light of data which must be derived from extensive studies in flowers and leaves, especially heterophylly and Alicean morphology of the epidermis. Features of flowers and leaf anatomy are therefore given sporadically in this treatment, due to lack of data for complete comparisons.

## CRITERIA FOR INCLUSION OF SPECIES IN *ANTIMIMA*

### Fruit

As demonstrated by Dehn (1989: 199), typical fruits of *Antimima* possess very large closing bodies filling and blocking the distal exit of the locule completely, i.e. no seeds can be expelled through this opening (Figure 1 C, F–H). In contrast, fruits of *Ruschia* have small, hook-shaped closing bodies which never form a complete blockage or barrier for the seeds.

In addition, expanding keels in fruits of *Antimima* are broad and lacinate, diverging distinctly in a  $\pm$  radial direction and reaching almost to the tip of the valve (Figure 1 C, H). In *Ruschia*, the expanding keels are typically shorter and are spread into an almost tangential direction, visible in the open capsule on the valve. Due to these structural differences, fruits of *Antimima* normally open completely (Figure 1 F), the valves often even recurving below the horizontal plane, whereas capsules of most species of *Ruschia* open their valves into an erect position only.

Covering membranes possess additional closing devices at their distal ends in both genera in principle. In fruits of *Ruschia* these devices appear mostly in the shape of closing rodlets, rarely as closing ledges or closing bulges. Closing rodlets can also occur in *Antimima*, but in this genus closing ledges (Figure 1 C, F) or the lack of any additional closing devices are more common (Figure 1 G, H). The last-mentioned condition is absent in *Ruschia*.

In seven species of *Antimima*, the covering membranes possess radial wings (Figure 1 G, H) or other protrusions on top, clearly visible in younger fruits. Similar features have been found in genera like *Cheiridopsis* N.E.Br., but never in typical fruits of *Ruschia*.

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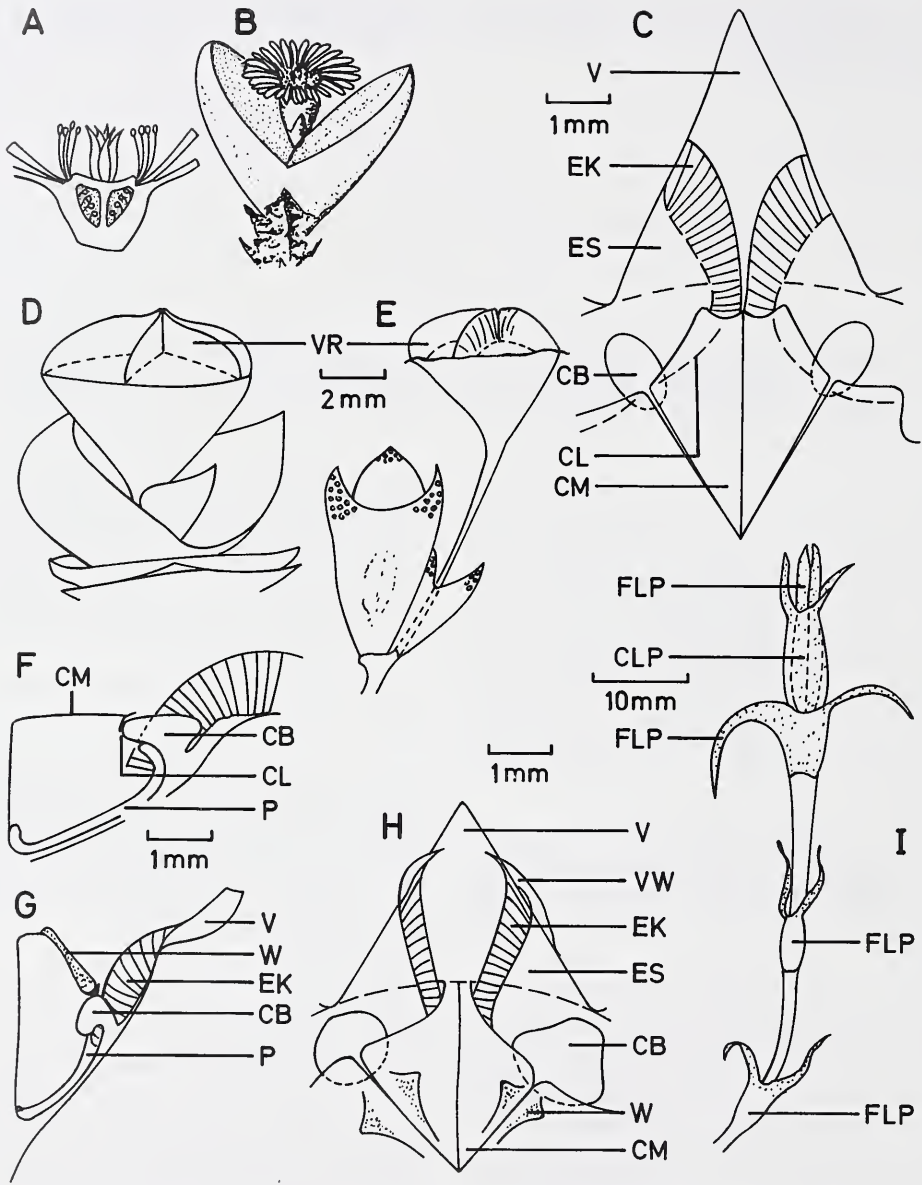


FIGURE 1.—A–D, *Antinima dualis*: A, l.s. through flower showing flat ovary surface and free stigmata, in contrast to *Argyroderma*; B, flowering branch with persisting old leaves below; C, part of open capsule with big closing bodies (CB), no valve wings, expanding keels (EK) diverging moderately and covering membranes (CM), with distinct closing ledge (CL) below near opening; D, side view of fruiting branch of herbarium material. A, B, figs of Brown 1930; C, Hartmann & Ihlenfeldt 4157 (HBG); D, Peers NBG 370/33 (BOL!), holotype of *A. villetii*. E, *A. pumila*, Hartmann 30325 (HBG!), side view of fruiting heterophyllous branch: long connate sheath is papery and smooth, short erect free parts papillate. F, *A. dolomitica*, Dinter 3782 (BOL, iso.), radial l.s. through capsule in middle of locule: straight covering membrane (CM) lying distally on big closing body (CB), which is also touched by closing ledge (CL). G, *A. fenestrata*, Hartmann & Dehn 15626 (HBG!), radial l.s. through capsule in middle of locule: covering membranes sloping down from a high centre ending in a distal recurving pressed against big white closing body (CB); erect wing in nearly radial position stabilizing covering membrane. H, *A. eendornensis*, Dinter 5207 (B, holo!), part of open capsule with basally distant moderately diverging expanding keels (EK), small valve wings (VW) broadest in middle, very big closing bodies (CB) and covering membranes (CM) pressed against them; covering membranes with radial wings on top lowering towards centre. I, *A. distans*, Hartmann et al. 20682: heterophyllous long shoot with several leaf pairs with short connate sheaths and free long parts (FLP) and connate subterminal leaf pair (CLP) forming long sheath with short free parts enclosing terminal leaf pair. ES, expanding sheet; P, placenta; V, valve; VR, valve rim; W, wing on top of covering membrane.



Fruits of the majority of species of *Ruschia* lack valve wings altogether, with a few exceptions such as *Ruschia* subgenus *Spinosa*. Capsules of *Antimima* are also mostly devoid of valve wings (Figure 1C), but in a number of species narrow, awn-shaped or even broader valve wings are found, always broadest in the middle and tapering towards both ends (Figure 1H).

Finally, fruits of *Ruschia* develop a long, deep fruit base whereas those of *Antimima* have rather shallow, mostly bowl- or funnel-shaped capsule bases (Figure 1D, E).

Locule numbers are mostly five in both genera, six occurring in several species in *Ruschia* and in *Antimima*.

### Leaves

Isophylly (i.e. all leaves of a plant are  $\pm$  equal), is present in all species of *Ruschia*. In contrast, the species of *Antimima* develop isophylly (Figure 1B, D) or heterophylly on a plant, the latter either as a result of two leaf pairs (Figure 1E) of different leaf shapes developing in one season, or as a result of differing leaf shapes developing in sequence along a side branch (Figure 1I). The first condition resembles that in *Cheiridopsis* subg. *Cheiridopsis* (Hartmann & Dehn 1987) or *Mitrophyllum* (Poppendieck 1976). Leaves developing in sequence along a side branch resemble those of *Vanzijlia* L. Bolus (Hartmann 1983). In both cases, the long-sheathed leaf pair forms a papery, persisting sleeve-like protective cover enveloping the subsequent, assimilating leaf pair during the dry season. The dry, persistent sheath consists mostly of the connate lower parts of the leaves of a pair (Figure 1E, I), but in a few cases the leaves are separated to the base but stand closely together forming a protective sleeve-like cover. In these cases, the broad lower parts resemble sheaths that have been slit open, but they were never connate, and the upper parts resemble the free parts of sheathed leaves closely. In general, the epidermis of the sheaths is smoother than that of the free tips, and often the different leaf types differ in their epidermal structures.

### Flowers

Flowers of both genera are rather small in the majority of species, rarely exceeding 20 mm in diameter (Figure 1A, B). The petals are white to pink or purple and often arranged in five, rarely six, distinctive groups. Filamentous staminodes are present, surrounding the central cone of stamens. In many cases, the tips elongate and recurve, and are often dark purple to almost black in colour. Characters of the flowers do not differ in principle between *Ruschia* and *Antimima*, neither do inflorescences, which can be solitary or in cymes of various sizes, typical of species but not of either genus.

### Growth forms

After the removal of a number of compact species from *Ruschia* by Glen (1986: *Ebracteola* Schwantes, *Acrodon* N.E.Br.) and the re-establishment of *Marlothiella* Schwantes (Hammer 1995), *Ruschia* comprises almost exclusively, shrubby to creeping growth forms with long, visible internodes and branching at the distal ends of the stems.

In *Antimima*, growth forms are variable: compact to caespitose, rarely creeping, or with a compact centre with long shoots climbing into other shrubs. All shrubs with a marked distal branching, proposed for inclusion in *Antimima* (by Dehn on herbarium sheets), had to be excluded from that genus because of their fruit morphology, which resembles that of *Ruschia*.

### CORRELATIONS BETWEEN CHARACTER STATES

The possession of the typical fruit permits a definite inclusion of a given plant in *Antimima*, but if fruits on the type sheet are absent or incomplete, the knowledge of the correlation of characters can also help to establish the identity of the material.

In all heterophyllous species with capsules, the expanding keels are basally separated, broad and lacinate, and diverging towards the tips of the valves, not in a tangential position as found in *Ruschia*. Valve wings are absent or present, mostly forming flanges tapering towards the tips. The closing bodies are mostly large, but in some species small white ones are present. In one species no closing body is developed but the capsules show so many similarities with those of other species that the taxon is included here in *Antimima*. Furthermore, it is deduced that heterophylly is correlated with the *Antimima* type of capsule morphology, and as a consequence, all heterophyllous species formerly belonging to the genus *Ruschia* are transferred to *Antimima*.

It should be noted that a revision of *Ruschia* down to species level is not yet available, the circumscription of that genus might therefore require some adjustment at a later stage. Nevertheless, based on the criteria given above, 95 species are transferred here from *Ruschia* to *Antimima*.

### TAXONOMY

***Antimima* N.E.Br.**, in The Gardeners' Chronicle ser. III, 87: 211 (1930); Dehn: 189 (1989); Hartmann & Stüber: 1 (1993); Hartmann: 229 (1996). Type species: *A. dualis* N.E.Br.

Plants compact, caespitose or with compact centre and long shoots, isophyllous or heterophyllous. *Leaves*: cymbiform with convex sides to nearly finger-shaped, often keeled in upper part; or mostly oval and very often connate for at least part of the length, leaf pairs differing in this feature, mucronate; epidermis cells flat to papillate, wax cover smooth or papillae, with a smooth lateral channel and wax flakes or platelets on rest of surface. *Flowers*: 1(–3), rarely in well-developed cymes; bracts and bracteoles present; petals pink to purple, rarely white, often arranged in 5 (rarely 6) groups. *Filamentous staminodes*: mostly in a central cone surrounding stamens closely. *Capsules*: 5, rarely 6 locules, stalked, always with persisting bracteoles, top with high or low valve rims, base mostly bowl-shaped, sometimes funnel-shaped; covering membranes undulate, more rarely straight, mostly elevated in centre, in several species with radial or tangential wings or other protrusions on them; closing body large, rarely small, absent in one species; expanding keels broad, diverging and radial in distal part, reaching to tip of valve; valves with or without mostly narrow valve wings.

## DISTRIBUTION

From Lüderitz and Warmbad, Namibia; southwards to the Northern Cape, Free State, Western Cape, and Eastern Cape, South Africa.

The following species are included in *Antimima* as circumscribed above, most of them transferred from the genus *Ruschia*.

1. *Antimima addita* (L.Bolus) H.E.K.Hartmann, comb. nov.

*Ruschia addita* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 284 (1931). Type: *M. Schlechter 8427* (BOL, holo.).

Plants compact with long shoots, isophyllous. *Leaves*: terete, mucronate. *Capsules*: typical in all respects. Typical of species: rich cymes.

2. *Antimima alborubra* (L.Bolus) Dehn in Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg 22: 212 (1989). Type: *Herre 8861* (BOL, holo.).

*Ruschia alborubra* L.Bolus: 494 (1934).

Plants with compact centre from which  $\pm 5$  long shoots rise, isophyllous. *Leaves*: trigonous to cymbiform. *Capsules*: typical in all respects. Typical of species: very big basal leaves and rather small flowers, smaller than calyx.

3. *Antimima amoena* (Schwantes) H.E.K.Hartmann, comb. nov.

*Ruschia amoena* Schwantes in Monatsschrift der Deutschen Kakteen-Gesellschaft 2: 66 (1930). Type: *Anon. s.n.*, photograph of flowering 'type plant' in collection Schwantes (HBG, lecto., here designated).

Plants compact to caespitose, isophyllous. *Leaves*: trigonous, aristate. *Capsules*: typical in all respects. Typical of species: distinct darker lines along keel and margins.

4. *Antimima androsacea* (Marloth & Schwantes) H.E.K.Hartmann, comb. nov.

*Ruschia androsacea* Marloth & Schwantes in Zeitschrift für Sukkulantenkunde 3: 299 (1928). *Mesembryanthemum androsaceum* Marloth: 19 (1927) nom. nud. *Ruschia androsacea* (Marloth) Schwantes: 19 (1927) nom. nud. *Mesembryanthemum androsaceum* (Schwantes) N.E.Br.: 32 (1930). Type: *Marloth 9682* (HBG, holo.).

Plants forming flat mats, isophyllous. *Leaves*: forming white bodies in the resting state. *Capsule*: top almost flat, base short, funnel-shaped, closing body round, white, rather small for genus; covering membranes convex with a low distal rim, a closing ledge below it, bases of expanding keels just not touching each other at their bases, moderately diverging and tapering into short awns. Typical of species: leaves of a pair form small, brightly white bodies in the dry state.

5. *Antimima argentea* (L.Bolus) H.E.K.Hartmann, comb. nov.

*Ruschia argentea* L.Bolus in Journal of South African Botany 27: 52 (1960). Type: *Hall 1883* (BOL, holo.).

Plants compact, isophyllous. *Leaves*: triquetrous with pointed tip, grey from papillae. *Capsules*: typical of genus. Typical of species: awl-shaped silvery to grey leaves.

6. *Antimima aurasensis* H.E.K.Hartmann in Kakteen und andere Sukkulanten 47: 231 (1996). Type: *Hartmann et al. 20865* (HBG, holo.).

Plants caespitose, elongate branches formed when not eaten, isophyllous. *Leaves*: triquetrous. *Capsules*: typical of genus. Similar to *A. perforata* in growth and leaves, but capsules with 5 locules only.

7. *Antimima biformis* (N.E.Br.) H.E.K.Hartmann, comb. nov.

*Mesembryanthemum biforme* N.E.Br. in Kew Bulletin 1929: 58 (1929). *Ruschia biformis* (N.E.Br.) Schwantes: 230 (1938). Type: *Muir s.n.* (K, holo.).

Plants caespitose, heterophyllous. *Leaves*: sheath of one leaf pair forming a body with two very short lobes, other leaf pair almost free, conspicuously dotted. *Capsules*: with expanding keels diverging and transgrading into expanding sheets, closing body knob-shaped. Typical of species: dotted, connate leaves of one pair.

8. *Antimima bina* (L.Bolus) H.E.K.Hartmann, comb. nov.

*Ruschia bina* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 282 (1931). Type: *Pillans BOL19610* (BOL, holo.).

Spreading shrubs to 150 mm high, internodes reddish, heterophyllous. *Leaves*: sheath of one leaf pair oval, white, keel of each leaf running down sheath as a narrow wing, only tips papillate; second leaf pair basally connate for only  $\pm 2$  mm, densely papillate, leaves free on long shoots, oval sheaths always at base of short shoots, where both types of leaf pairs are formed alternatively. *Capsules*: with inconspicuous closing ledges, closing body medium-sized. Typical of species: leaves.

9. *Antimima bracteata* (L.Bolus) H.E.K.Hartmann, comb. nov.

*Ruschia bracteata* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 93 (1929). Type: *Erni BOL18921* (sheet 1) (BOL, lecto., here designated).

Plants are loose cushions, isophyllous. *Leaves*: trigonous, smooth. *Capsules*: typical of genus; covering membranes with remains of stiff wings in radial position. Typical of species: radial wings on covering membranes. Similar to *A. compacta*.

10. *Antimima brevicarpa* (L.Bolus) H.E.K.Hartmann, comb. nov.

*Ruschia brevicarpa* L.Bolus in Notes on Mesembryanthemum and allied genera, part 3: 279 (1954). Type: *Esterhuysen 20444* (BOL, holo.).

Plants creeping, later forming a mat, heterophyllous. *Leaves*: sheath of one leaf pair long, yellowish, rather smooth, enclosing larger part of subsequent leaf pair with a shorter connate part and longer free parts with papillae, in particular along margins and keel. *Capsules*: with closing bodies broader than thick, almost bean-shaped, covering membranes  $\pm$  straight with a low rim and closing ledges. Typical of species: creeping habit. Similar to *A. prostrata*, but larger-leaved.

**11. *Antimima brevicollis* (N.E.Br.) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum brevicolle* N.E.Br. in Kew Bulletin 1929: 58 (1929). *Ruschia brevicollis* (N.E.Br.) Schwantes: 230 (1938). Type: Muir 4064 (K, holo.).

Plants caespitose, heterophyllous. *Leaves*: sheath of one leaf pair connate for half its length, other pair with a short connate part. *Capsule*: not known.

**12. *Antimima buchbergensis* (Dinter) H.E.K.Hartmann, comb. nov.**

*Ruschia buchbergensis* Dinter in Monatsschrift der Deutschen Kakteengesellschaft 2: 219 (1930). Type: Dinter 6477A (HBG, lecto.), here designated: the three sheets of Dinter 6477 at HBG have been marked A, B, and C; A is chosen as the lectotype because it shows the typical caespitose growth and possesses fruits.

Plants compact to caespitose, isophyllous. *Leaves*: leaf pairs on lateral branches as pea-shaped bodies. *Capsules*: typical of genus, with very narrow valve wings. Typical of species: pea-shaped leaf pairs on proleptic shoots.

**13. *Antimima compacta* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia compacta* L.Bolus in Notes on Mesembryanthemum and allied genera, part 2: 144 (1929). Type: L.Bolus BOL18977 (BOL, holo.).

Plants compact, isophyllous. *Leaves*: trigonous with recurved tip. *Capsules*: typical of genus; covering membranes with stiff wings in radial position and tiny valve wings. Very similar to *A. bracteata*.

**14. *Antimima compressa* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia compressa* L.Bolus in Journal of South African Botany 27: 54 (1960). Type: Hall NBG1056/48 (BOL, holo.).

Plants caespitose with some long shoots, isophyllous. *Leaves*: trigonous, papillate. *Capsules*: typical of genus, valve wings very narrow. Typical of species: protruding, diagonal long shoots.

**15. *Antimima concinna* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia concinna* L.Bolus in Notes on Mesembryanthemum and allied genera, part 2: 123 (1929). *Mesembryanthemum comptum* N.E.Br.: 32 (1930). Type: Pillans NBG370/16 (BOL, lecto.), here designated; Mathews 1802/21 (BOL, paralecto.).

Plants compact, heterophyllous. *Leaves*: persisting yellow, papery sheath of one leaf pair around stem, free parts triquetrous, other leaf pair connate for 2–3 mm only, ending in recurved long awn; keels of leaves with distinct, large, long papillae. *Capsules*: typical of genus.

**16. *Antimima condensa* (N.E.Br.) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum condensum* N.E.Br. in Kew Bulletin 1929: 58 (1929). *Ruschia condensa* (N.E.Br.) Schwantes: 230 (1938). Type: Muir 4065 (K, holo.).

Plants caespitose, heterophyllous. *Leaves*: sheath of one leaf pair as a connate body with only short free tips during the resting period, whitish yellow, smooth, with a protruding roll along line where both leaves are fused in dry state; second leaf pair hardly connate, with elevations above subhypodermal idioblasts and a papillate epidermis. *Capsules*: typical of genus, valve wings narrow.

**17. *Antimima crassifolia* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia crassifolia* L.Bolus in Notes on Mesembryanthemum and allied genera, part 3: 338 (1958). Type: Hall BOL25758 (BOL, holo.).

Low shrubs with some erect flowering branches, isophyllous. *Leaves*: trigonous, thick. *Capsules*: typical of genus, 6-loculed.

**18. *Antimima dasyphylla* (Schltr.) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum dasyphyllum* Schltr. in Botanische Jahrbücher 27: 127 (1899). *Ruschia dasyphylla* (Schltr.) Schwantes: 20 (1927). Type: Schlechter 8773 (B, lecto.), here designated: one of the two sheets kept at B bears the note 'holotype' by Glen; it is here chosen as the lectotype.

*Ruschia concava* L.Bolus: 124 (1929). *Mesembryanthemum ciliolatum* N.E.Br.: 32 (1930). Type: Levyns 1375/26 (BOL, holo.).

Shrubs, heterophyllous. *Leaves*: sheath of one leaf pair long, orange-brown, free parts only 2–3 mm long, papillate; other leaf pair connate for 4 mm, free parts spreading, longer papillae on keel and margins. *Capsules*: typical of genus but expanding keels transgrading into expanding sheets and with distal awns. Typical of species: inconspicuous expanding keels.

**19. *Antimima defecta* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia defecta* L.Bolus in Journal of South African Botany 31: 85 (1965). Type: Van Heerde BOL27654 (BOL, holo.).

*Ruschia deflecta* L.Bolus ex Jacobsen: 491 (1970) orthographic variant.

Plants cushion-forming, heterophyllous. *Leaves*: yellow sheaths of one leaf pair on short shoots connate for  $\pm$  half their length, those on long shoots only connate for  $\pm$   $\frac{1}{6}$  of their length, free parts of both types with distant, big papillae. *Capsules*: typical of genus, but closing bodies hood-shaped and broader than thick. A deviating single fruit on the type sheet with broad valve wings and a longer base belongs to *Amphibolia*, but not to the remaining type material, which agrees with the description.



20. *Antimima dekenahi* (N.E.Br.) H.E.K.Hartmann, comb. nov.

*Mesembryanthemum dekenahi* N.E.Br. in Kew Bulletin 1929: 58 (1929). *Ruschia dekenahi* (N.E.Br.) Schwantes: 230 (1938). Type: *Dekenah* 23 (K, lecto.!, here designated); Muir 4079 (K, paralecto.!).

Plants compact to caespitose, isophyllous. *Leaves*: trigonous, mucronate. *Capsules*: typical of genus. Typical of species: fruits raised above plant and the thick root.

21. *Antimima distans* (L.Bolus) H.E.K.Hartmann, comb. nov.

*Mesembryanthemum distans* L.Bolus in Annals of the Bolus Herbarium 4: 89 (1927a). *Ruschia distans* (L.Bolus) L.Bolus: 236 (1950). Type: Anon. BOL18550 (BOL, holo.!).

Plants compact with erect, long shoots, heterophyllous. *Leaves*: sheath of one leaf pair long, almost smooth, with a bulge running down side where both leaves meet, and long,  $\pm$  triquetrous free parts with some large, long papillae along keel only; other leaf pair only slightly connate, free parts densely papillate. *Capsules*: typical of genus. Typical of species: stout, dark brown or maroon, long internodes (Figure 1I).

22. *Antimima dolomitica* (Dinter) H.E.K.Hartmann, comb. nov.

*Mesembryanthemum dolomiticum* Dinter in Feddes Repertorium 19: 150 (1923). *Corpuscularia dolomitica* (Dinter) Schwantes: 186 (1926). *Ruschia dolomitica* Dinter & Schwantes: 69 (1929). Type: Dinter 3782, Klinghardtberge (B, lecto.!, here designated); from Alicetal, Buntfeld-schuhplateau (B, BOL, paralecto.!).

Plants with compact base with erect, stiff long shoots bearing lateral proleptic bodies consisting of a hazelnut-shaped leaf pair each;  $\pm$  isophyllous. *Capsules*: typical of genus, closing bodies only medium-sized, as seen from above (Figure 1F). Typical of species: hazelnut-shaped leaf pairs.

23. *Antimima dualis* (N.E.Br.) N.E.Br., Gardeners' Chronicle, ser. III, 87: 211 (1930). Type: Pearson & Pillans 5483 (K, holo.!).

*Mesembryanthemum duale* N.E.Br.: 89 (1920). *Argyroderma duale* (N.E.Br.) N.E.Br.: 105 (1922).

*Ruschia dualis* L.Bolus: 104 (1929). Type: Hutchinson s.n. (BOL, lecto.!, here designated from three syntypes cited and placed on one sheet).

*Ruschia villetii* L.Bolus: 501 (1934) Type: Peers 1370/33 (BOL, holo.!).

Plants compact, highly branched, isophyllous. *Leaves*: trigonous but keeled, sides convex to straight, whitish grey. *Capsules*: typical of genus; covering membranes almost straight. The species can easily be confused with *A. turneriana*. Characteristic of *A. dualis* are the strictly compact growth, retained also in cultivation, and the strictly solitary flowers (Figure 1A–D).

24. *Antimima eendornensis* (Dinter) H.E.K.Hartmann, comb. nov.

*Mesembryanthemum eendornense* Dinter in Feddes Repertorium Beiheft 53: 86 (1928). Type: Dinter 5207 (B, holo.!).

Semi-compact dwarf shrublets, isophyllous. *Leaves*: triquetrous with long papillae. *Capsules*: typical of genus with narrow valve wings at the point where they touch edge of valve and with oblique wings on top of covering membranes, 6-loculed (Figure 1H).

Dinter (1928: 86, 87) did not give a formal description, only a short diagnosis in contrast to *Mesembryanthemum hospitale* (now a member of *Ruschia* subgenus *Spinosa*). The type sheet at B had been wrongly placed with *A. quarzitica* up to now.

25. *Antimima elevata* (L.Bolus) H.E.K.Hartmann, comb. nov.

*Ruschia elevata* L.Bolus in Notes on Mesembryanthemum and allied genera, part 2: 305 (1931). Type: Luckhoff BOL19873 (BOL, holo.!).

Plants caespitose, isophyllous. *Leaves*: with broadly trigonous, rough to warty free parts, greyish. *Capsules*: typical of genus; covering membranes raised high in centre and closing bodies bean-shaped and rather small.

26. *Antimima emarcescens* (L.Bolus) H.E.K.Hartmann, comb. nov.

*Ruschia emarcescens* L.Bolus in Notes on Mesembryanthemum and allied genera, part 3: 281 (1954). Type: Acocks 16995 (BOL, holo.!). *Ruschia emarcescens* L.Bolus ex Jacobsen: 492 (1970) orthographic variant.

Plants with compact centre with long shoots, heterophyllous; roots thickened and forming elongate, potato-shaped tubers. *Leaves*: one leaf pair with dry, papery sleeve-like covers longer than free parts, but not connate; other leaf pair with sheaths shorter than free parts, smooth, papery during dry season, free parts triquetrous, with low papillae, turning dark when drying, both types 7–10 mm long. *Capsules*: typical of genus with high valve rims.

27. *Antimima erosa* (L.Bolus) H.E.K.Hartmann, comb. nov.

*Ruschia erosa* L.Bolus in Notes on Mesembryanthemum and allied genera, part 3: 279 (1954). Type: Acocks 17126 (BOL, holo.!).

Plants densely shrubby, isophyllous. *Leaves*: terete, apically rounded. *Capsules*: typical of genus; covering membranes straight; valve wings very narrow. Resembles species of *Rhinephyllum* in growth form, both occur in the same area, so that they can easily be confused.

28. *Antimima evoluta* (N.E.Br.) H.E.K.Hartmann, comb. nov.

*Mesembryanthemum evolutum* N.E.Br. in Kew Bulletin 1913: 120 (1913). *Ruschia evoluta* (N.E.Br.) L.Bolus: 178 (1928a). Type: Pearson 5946 (K, holo.!).

Plants compact, white in the resting state, heterophyllous. *Leaves*: sheath of one leaf pair forming white body in dry season, smooth, keel markedly smooth, margins ciliate, completely embracing subsequent leaf pair with longer free parts with short papillae on them. *Capsules*: with closing body pointing into locule like a finger; expanding keels very similar to the short ones of *A. dualis*.

**29. *Antimima exsurgens* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia exsurgens* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 280 (1931). Type: *L.Bolus BOL19334* (BOL, holo.).

Plants with compact centre and long shoots, each internode with papery whitish apical rim, appearing corky below and drying into rings, stems therefore resembling cones put one into the other, heterophyllous. *Leaves*: sheath of one leaf pair turning papery for most of its length ( $\pm 6$  mm) in the resting state, free apical part of  $\pm 2$  mm with very low papillae; second leaf pair enveloped during the resting period,  $\pm 6$ –8 mm long, triquetrous, epapillate; in both leaf types keel and margins rounded. *Capsules*: typical of genus.

**30. *Antimima fenestrata* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia fenestrata* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 281 (1931). Type: *Luckhoff BOL19612* (BOL, holo.).

Compact shrubs forming tiny tree-like shapes, heterophyllous. *Leaves*: sheath of one leaf pair long, smooth, white, embracing subsequent leaves at bases, these latter free for  $\pm 1/2$  their length and withering in a peculiar way: hardened bundles along keel (and into the apical tooth) and margins form a triangular window frame and persist much longer than intermediate tissue so that finally triangular openings are formed. *Capsules*: typical of genus; highly undulate covering membranes with very broad, horizontally arranged wings on top almost completely hiding covering membranes when seen from above (Figure 1G). Typical of species: windowed leaves drying white, with frames remaining on plants.

**31. *Antimima fergusoniae* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia fergusoniae* L.Bolus in South African Gardening and Country Life 18: 279 (1928b). *Mesembryanthemum fergusoniae* (L.Bolus) N.E.Br.: 32 (1930). Type: *Ferguson BOL1882* (sheet 1) (BOL!).

Plants caespitose, heterophyllous. *Leaves*: both pairs forming sheaths, one pair with pronounced bulges above tannin idioblasts and low papillae; second pair with lower bulges but longer papillae. *Capsules*: typical of genus.

After the first description in English in September 1928 (Bolus 1928b), Bolus published a Latin description of the species as well in November 1928 (Bolus 1928d: 7), where she cited the type. Nevertheless, the description in September fulfills all requirements for the new combination to be validly published, at that time.

**32. *Antimima gracillima* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*R. gracillima* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 203 (1930). Type: *Frames BOL 19208* (BOL, holo.).

Plants compact with decumbent long shoots, heterophyllous. *Leaves*: sheaths of leaf pairs on short shoots connate for  $\pm 1/2$  their length, those on long shoots for  $\pm$

$1/4$ , free parts of both types with distant, big papillae, aristate. *Capsules*: not known.

**33. *Antimima granitica* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum graniticum* L.Bolus in Annals of the Bolus Herbarium 4: 88 (1927a). *Ruschia granitica* (L.Bolus) L.Bolus: 221 (1950). Type: *Pillans BOL17772* (BOL, holo.).

Plants caespitose, isophyllous. *Leaves*: trigonous, apically roundish. *Capsules*: typical of genus; valve wings very narrow.

**34. *Antimima hallii* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia hallii* L.Bolus in Notes on Mesembryanthemum and allied genera, part 3: 218 (1950). Type: *Hall BOL24059* (BOL, lecto., here designated); *Peers BOL 24060* (BOL, paralecto.).

Plants with compact centre with long shoots, erect at first, decumbent later, rooting at nodes some distance from the primary centre and developing a secondary compact centre, heterophyllous. *Leaves*: sheaths of both types of leaves papery, white, disintegrating early; bases of second leaf pair almost separated by a triangle of stem tissue, with low papillae, old leaves closely set on short shoots. *Capsules*: typical of genus. Typical of species: formation of secondary compact centres with adventitious roots.

**35. *Antimima hamatilis* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia hamatilis* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 106 (1929). *Mesembryanthemum hamatile* (L.Bolus) N.E.Br.: 32 (1930). Type: *Pillans 6080* (BOL, holo.).

Plants with decumbent branches, heterophyllous. *Leaves*: sheath of one leaf pair connate for  $\pm 1/2$  its length, free parts papillate, mucro to 1 mm long; second leaf pair connate for  $1/6$  of its length, free parts papillate, longer papillae along keel and margins, these leaves forming repeatedly on fresh long shoots. *Capsules*: unknown.

**36. *Antimima hantamensis* (Engler) H.E.K.Hartmann & Stüber, Contributions from the Bolus Herbarium 15: 68 (1993). *Mesembryanthemum hantamense* Engl.: 190 (1909) Type: *Meyer s.n.* (B, holo.).**

*Ruschia disarticulata* L.Bolus: 286 (1931). *Eberlanzia disarticulata* (L.Bolus) L.Bolus: 387 (1958) Type: *L.Bolus 19335* (BOL, holo.).

*Ruschia stellata* L.Bolus: 140 (1927/1928). *Mesembryanthemum stellans* (L.Bolus) N.E.Br.: 32 (1930). *Eberlanzia stellata* L.Bolus nom. nud. Type: *Compton 1414/27* (BOL, holo.).

Flat shrubs smelling of fish when damaged, covered in spines derived from big dichasial inflorescences, isophyllous. *Leaves*: trigonous. *Capsules*: with high valve rims extending over edge of capsule, otherwise with typical features. Plants always densely covered with spines, making it easy to recognise them.

**37. *Antimima herrei* (Schwantes) H.E.K.Hartmann, comb. nov.**



*Ruschia herrei* Schwantes in Zeitschrift für Sukkulentenkunde 3: 301 (1928a). *Mesembryanthemum herrei* (Schwantes) N.E.Br.: 32 (1930). Type: Karrooport Ceres, *H. Herre* in *Bot. Gard. Stellenbosch* 1876. As this could not be traced, the following lectotype is designated: *Anon. s.n.* (HBG!), photograph of 'my type plant' in collection Schwantes HBG).

Plants compact, heterophyllous. *Leaves*: sheath of one leaf pair papery for most of its length; other leaf pair free (flowering plant on photograph showing free leaves only), as is the case during the growing and flowering period. *Capsules*: typical of genus; covering membranes with low protrusions in radial direction near centre of fruit. Placed by Schwantes (1928a: 302) in a group called '*Ruschia*', not described formally, together with '*R. ventricosa*' and '*R. schlechteri*', both also heterophyllous.

**38. *Antimima intervallis* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia intervallis* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 91 (1929). Type: *Pillans 6056* (BOL, holo.!).

Shrubs with decumbent branches, heterophyllous. *Leaves*: first leaf pair with long, loose sheaths enclosing subsequent leaves; other leaf pair hardly connate, both glabrous, green; epidermis papillate, epidermis cells with lower papillae on smaller leaves. *Capsules*: typical of genus; valve wings or very narrow bands appearing only when a fresh fruit is opening. In the leaf sequence, the species resembles that of *Vanzijlia annulata*. The citation of the name *Ruschia intervallis* L.Bolus under *Mossia intervallis* is an error (Brown 1930: 71, 151).

**39. *Antimima ivori* (N.E.Br.) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum ivori* N.E.Br. in Kew Bulletin 1929: 58 (1929). *Ruschia ivori* (N.E.Br.) Schwantes: 230 (1938). Type: *Dekenah 67* (K, lecto.!, here designated); *Muir 4285* (K, paralecto.!).

Plants with flat mats, heterophyllous. *Leaves*: sheath of one leaf pair smooth, white in its lower half, often suffused purplish, tips disintegrating into thread-like protruberances, sheath enclosing subsequent leaf pair of papillate leaves connate only for  $\pm 1/3$  of its length; surface of epidermis of outer leaf pair of elongate cells with cuticular folds covered by an almost continuous wax layer. *Capsules*: typical of genus, but top with low rims, 6-lobed. Typical of species: lacinate upper parts of highly connate leaf pairs persisting on plant for many years. In this feature, and in leaf surfaces, it resembles *A. pygmaea* most closely, differing in the truncate leaf tips and in fruit morphology from the latter.

**40. *Antimima karroidea* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia karroidea* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 306 (1931). Type: *Archer 364* (BOL, holo.!).

Plants compact with long decumbent shoots, numerous short shoots on them, heterophyllous. *Leaves*: sheath of one leaf pair whitish, keel of shorter free part continuing as a row of long papillae on sheath and internode below; alternating leaf pair with a sheath only 1.5 mm

long, free parts subulate. *Capsules*: typical of genus; expanding keels merging into expanding sheets. Similar in leaf shapes and sequence to *A. fergusoniae*.

**41. *Antimima klaverensis* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum klaverensis* L.Bolus in Annals of the Bolus Herbarium 4: 96 (1927a). *Ruschia klaverensis* (L.Bolus) Schwantes: 58 (1949). Type: *Compton NBG291/22* (BOL, holo.!).

Plants caespitose, smelling of fish, isophyllous. *Leaves*: trigonous to terete. *Capsules*: typical of genus. Leaves, fruit and growth form agree well with those of *A. watermeyeri*, which lacks a fishy smell.

**42. *Antimima koekenaapensis* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia koekenaapensis* L.Bolus in Journal of South African Botany 28: 299 (1962). Type: *Hall 2398* (BOL, holo.!).

Plants compact with long shoots, these in turn with short shoots bearing flowers appearing in bundles or dense groups in the following year, isophyllous. *Leaves*: triquetrous, pointed. *Capsules*: typical of genus. Typical of species: tufted short flowering shoots.

**43. *Antimima komkansica* (L.Bolus) H.E.K. Hartmann, comb. nov.**

*Ruschia komkansica* L.Bolus in Journal of South African Botany 28: 298 (1962). Type: *Hall 2550* (BOL, holo.!).

Shrubs up to 600 mm high, isophyllous. *Leaves*: trigonous. *Capsules*: typical of genus; very narrow valve wings and low radial wings on covering membranes. Plants very tall for genus.

**44. *Antimima lawsonii* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum lawsonii* L.Bolus in Annals of the Bolus Herbarium 4: 85 (1927a). *Ruschia lawsonii* (L.Bolus) L.Bolus: 219 (1950). Type: *Lawson 18551* (BOL, holo.!).

Plants compact, isophyllous. *Leaves*: triangular to triquetrous, light grey, hard. *Capsules*: most similar to those of *A. dualis*, but closing body smaller and almost hook-shaped. Grows far from most other species of genus, settling in distinct, stony habitats on limestone and seemingly unable to explore adjacent areas with a sand cover where grass and trees predominate.

**45. *Antimima leipoldtii* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia leipoldtii* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 61 (1929). *Mesembryanthemum leipoldtii* (L.Bolus) N.E.Br.: 32 (1930). Type: *Leipoldt BOL18905* (BOL, holo.!).

Low shrubs, heterophyllous. *Leaves*: sheath of one leaf pair long, smooth, long free parts with some big papillae along keel only; other leaf pair short, with long papillae. *Capsules*: typical of genus; valves with distinct narrow wings broadest at middle.



**46. *Antimima leucanthera* (L.Bolus) H.E.K. Hartmann, comb. nov.**

*Mesembryanthemum leucantherum* L.Bolus in Annals of the Bolus Herbarium 4: 7 (1925). *Ruschia leucanthera* (L.Bolus) L.Bolus: 239 (1927b). Type: Tugwell BOL17108 (BOL, lecto., here designated); Russell NBG8/24 (BOL, paralecto.).

Plants compact to caespitose, isophyllous, hypocotyl and roots thickened. *Leaves*: trigonous, mucronate. *Capsules*: typical of genus, interior falling off persistent old outer bundles of capsule, leaving a prickly star on plant where a fruit has been; in young fruits narrow valve wings in angle where expanding keel meets edge of valve. In habitat, plants adorned by whitish capsules for most of year. Similar to *A. dekenahi*, but differing in wings on covering membranes and longer papillae along keel and margins of leaves.

**47. *Antimima limbata* (N.E.Br.) H.E.K. Hartmann, comb. nov.**

*Mesembryanthemum limbatum* N.E.Br. in Kew Bulletin 1929: 59 (1929). *Ruschia limbata* (N.E.Br.) Schwantes: 230 (1938). Type: Marloth 13173 (K, holo!).

Plants creeping, isophyllous. *Leaves*: trigonous with convex sides, keel and margin reddish brown. *Capsules*: typical of genus. Leaves dry beautifully with reddish margins. Creeping growth forms are rare in *Antimima*.

**48. *Antimima lodewykii* (L.Bolus) H.E.K. Hartmann, comb. nov.**

*Ruschia lodewykii* L.Bolus in Notes on Mesembryanthemum and allied genera, part 3: 218 (1950). Type: L.van Heerde (3) BOL 23640 (BOL, lecto., here designated: chosen from several sheets).

Plants compact, heterophyllous. *Leaves*: sheath of one leaf pair white, smooth, free tips papillate; second leaf pair also highly connate, but entirely papillate, only bulging keel and margins apically smooth, enclosed during the resting state. *Capsules*: typical of genus; closing bodies shaped like heads of snakes and small. Typical of species: very tight arrangement of old leaves, like pieces of meat on a spit.

**49. *Antimima loganii* (L.Bolus) H.E.K. Hartmann, comb. nov.**

*Ruschia loganii* L.Bolus in Notes on Mesembryanthemum and allied genera, part 3: 61 (1937). Type: Logan 31 (BOL, holo!).

Plants caespitose, white during the dry season, heterophyllous. *Leaves*: sheath of one leaf pair long, smooth, with short, free parts with papillae; other leaf pair only a little connate, free parts trigonous, papillate, apiculate, both  $\pm 9$  mm long. *Capsules*: typical of genus; narrow valve wings. Typical of species: raised, star-shaped fruits above the white tiny shrub during dry season.

**50. *Antimima lokenbergensis* (L.Bolus) H.E.K. Hartmann, comb. nov.**

*Ruschia lokenbergensis* L.Bolus in Journal of South African Botany 30: 239 (1964). Type: Esterhuysen 30699 (sheet 1) (BOL, lecto., here designated: chosen from 2 sheets).

Shrubs to 450 mm high, isophyllous. *Leaves*: elongate-ovate. *Capsules*: typical of genus. Almost free leaves unusually rounded for genus.

**51. *Antimima longipes* (L.Bolus) Dehn in Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg 22: 211 (1989). Type: Pillans 5811 (BOL, holo!).**

*Ruschia longipes* L.Bolus: 256 (1927b). *Mesembryanthemum longipes* (L.Bolus) N.E.Br.: 32 (1930).

Plants are caespitose cushions to  $\pm 80$  mm high, isophyllous. *Leaves*: slender, trigonous. *Capsules*: on pedicels 60 mm long; covering membranes with large horizontal wings forming a second layer over them, closing ledges low and inconspicuous; closing body typical. Typical of species: fruit morphology with valve wings and radial wings on covering membranes plus presence of big white closing bodies.

**52. *Antimima luckhoffii* (L.Bolus) H.E.K. Hartmann, comb. nov.**

*Ruschia luckhoffii* L.Bolus in Notes on Mesembryanthemum and allied genera, part 2: 283 (1931). Type: Luckhoff 19611 (BOL, holo!).

Plants caespitose, heterophyllous. *Leaves*: one leaf pair with brown sheath at base and with 2–3 mm long free parts densely covered with low papillae, tip thus forming a  $\pm$  triangular top; other leaf pair with short sheath 5–6 mm long, free parts with translucent margins and keel. *Capsules*: not known.

**53. *Antimima maleolens* (L.Bolus) H.E.K. Hartmann, comb. nov.**

*Ruschia maleolens* L.Bolus in Notes on Mesembryanthemum and allied genera, part 2: 22 (1928d). *Mesembryanthemum maleolens* (L.Bolus) N.E.Br.: 32 (1930). Type: Pillans BOL17796 (BOL, holo!).

Shrubs up to 250 mm high smelling of salted fish, isophyllous. *Leaves*: trigonous. *Capsules*: typical of genus.

**54. *Antimima maxwellii* (L.Bolus) H.E.K. Hartmann, comb. nov.**

*Ruschia maxwellii* L.Bolus in Notes on Mesembryanthemum and allied genera, part 2: 106 (1929). *Mesembryanthemum maxwellii* (L.Bolus) N.E.Br.: 32 (1930). Type: M.Bolus BOL18939 (BOL, holo!).

Plants with compact centre with long shoots and highly branched, tufted short shoots, bearing flowers (and fruits) in groups, heterophyllous. *Leaves*: smooth, papery sheath of one leaf pair of  $\pm 5$  mm length enclosing base of subsequent leaf pair with sheath of  $\pm 4$  mm and free parts up to 15 mm long; epidermis cells of free parts almost flat, only slightly protruding. *Capsules*: typical of genus; covering membranes raised high near centre and with indications of radial protrusions, but these appear as if folded and not forming a wing proper. Typical of species: dense groups of short shoots developing on long shoots.

**55. *Antimima menniei* (L.Bolus) H.E.K. Hartmann, comb. nov.**

*Ruschia menniei* L.Bolus in Journal of South African Botany 31: 86 (1965). Type: Mennie BOL27660 (BOL, holo!).

Plants caespitose with erect branches, heterophyllous. *Leaves*: short, smooth sheath of one type of leaf pair persisting as envelopes around stem, long, free parts with big, distant papillae; bracteoles without a sheath, leaves almost separated by tissue of pedicel. *Capsules*: typical of genus; expanding keels transgrading into expanding sheets.

**56. *Antimima mesklipensis* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia mesklipensis* L.Bolus in Notes on Mesembryanthemum and allied genera, part 2: 281 (1931). Type: *Mathews (Ryder) NBG2250/30* (BOL, holo.).

Plants caespitose, heterophyllous. *Leaves*: one leaf pair with greyish brown sheath, 2–3 mm long, free parts distantly papillate; other leaf pair connate for < 1 mm, free parts broadly trigonous, densely papillate. *Capsules*: not known. Resembles *A. persistens* in persistence of old (longer) leaves.

**57. *Antimima meyeri* (Schwantes) H.E.K.Hartmann, comb. nov.**

*Ruschia meyeri* Schwantes in Monatsschrift der Deutschen Kaktengesellschaft 2: 64 (1930). Type: *Anon. s.n.* (HBG, lecto.), here designated: photograph of the 'type plants' in collection Schwantes HBG).

Compact shrublets, heterophyllous with 3 different types of leaves. *Leaves*: most commonly sheaths whitish yellow with reddish brown free tips; epidermis at tips with rounded, low papillae; leaves up to 8 mm long; at bases of side branches first leaf pair with a white-yellow sheath, but without any different free tips,  $\pm 5$  mm long; second leaf pair hardly connate, free parts with prominent, long papillae giving leaves a rough appearance,  $\pm 5$  mm long. *Capsules*: very hard, differing from typical form by possession of small finger-shaped closing bodies. Typical of species: formation of at least three different leaf forms and development of four new branches under terminal fruit, in contrast to common pattern of two or single branch.

**58. *Antimima microphylla* (Haw.) Dehn in Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg 22: 213 (1989). Type: drawing by Duncanson [K, lecto.], designated by Dehn: 213 (1989).**

*Mesembryanthemum microphyllum* Haw.: 73 (1803). *Ruschia microphylla* (Haw.) Schwantes: 20 (1927).

Low shrublets, heterophyllous. *Leaves*: set densely, keels cartilaginous. *Capsule*: not known.

**59. *Antimima minima* (Tischer) H.E.K.Hartmann, comb. nov.**

*Cheiridopsis minima* Tischer in Succulenta 9: 145 (1927). Type: *Anon. s.n.* (HEID).

Plants compact, isophyllous. *Leaves*: trigonous. *Capsules*: typical of genus. Description of fruit permits the conclusion that the species belongs to *Antimima*, where in several species, centrally raised covering membranes occur combined with deep-set, white, flat closing bodies.

**60. *Antimima minutifolia* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia minutifolia* L.Bolus in Journal of South African Botany 30: 239 (1964). Type: *Hall 2829* (BOL, holo.).

Dark shrublets, outer long shoots decumbent, heterophyllous. *Leaves*: long sheath of one leaf pair turning white, basally maroon, free parts 1–2 mm long, papillate; second leaf pair hardly connate, free parts 3–4 mm long, papillate and ciliate along margins, latter leaves on long shoots, sheaths always at bases of short side shoots, on which both leaf types alternate regularly. *Capsules*: typical of genus. Typical of species: dark appearance as a result of dark stems which are well visible because leaves are very short.

Distinguished from *A. distans* from the same area by much more slender stems and a broad cushion shape with age. The first description appeared in June 1928, being validly published at that time; the Latin description appeared in August 1928 (Bolus 1928c), but was superfluous at that time.

**61. *Antimima modesta* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia modesta* L.Bolus in Notes on Mesembryanthemum and allied genera, part 3: 105 (1937). Type: *Holloway 63* (BOL, holo.).

*Ruschia modesta* L.Bolus forma *glabrescens* L.Bolus: 54 (1960). Type: *Geyer SUG13973* (BOL, holo.).

Plants compact with long, erect, stiff shoots, isophyllous. *Leaves*: boat-shaped with convex sides. *Capsules*: typical of genus. The name should be used for stout plants with few to some flowers per inflorescence from a restricted area north of the Gariep River in Namibia.

**62. *Antimima mucronata* (Haw.) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum mucronatum* Haw. in Miscellanea naturalia: 73 (1803). *Ruschia mucronata* (Haw.) Schwantes: 20 (1927). Type: drawing 980/203 of Duncanson (K, lecto.), here designated).

*Ruschia mathewsii* L.Bolus: 139 (1927/1928). Type: *Mathews NBG 1893/24* (BOL, holo.).

Plants compact with decumbent long shoots, heterophyllous. *Leaves*: sheath of one leaf pair smooth, later white, thin, papery, keel markedly horny, ciliate to serrulate; second leaf pair connate for 1–2 mm only, free parts  $\pm 10$  mm long, with distinct awn borne apically, with low papillae, keel ciliate to serrulate, wax in dense layers of vertical platelets on free parts. *Capsules*: typical of genus; expanding keels merging gradually into expanding sheets.

The drawing of Duncanson (K!) shows a plant in the growing season with several long shoots (with prominent internodes) with shortly connate, spreading leaves, resembling those of long shoots of *A. mathewsii* very closely.

**63. *Antimima mutica* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia mutica* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 61 (1929). *Mesembryanthemum muticum* (L.Bolus) N.E.Br.: 32 (1930). Type: *Pillans BOL18898* (BOL, holo.).

Compact shrublets, heterophyllous. *Leaves*: sheath of one leaf pair white,  $\pm 4$  mm long, free tips  $\pm 3$  mm long, covered by fine papillae, longer ones on margins; second leaf pair with a 1–2 mm long sheath, free parts  $\pm 6$  mm long, papillate, the latter on long shoots, short shoots beginning with a sheathed leaf pair, later both types alternating regularly. *Capsules*: typical of genus. Smaller-leaved version of *A. peersii*.

**64. *Antimima nobilis* (Schwantes) H.E.K.Hartmann, comb. nov.**

*Ruschia nobilis* Schwantes in Monatsschrift der Deutschen Kakteen-gesellschaft 2: 65 (1930). Type: *M. Schlechter s.n.* (HBG, collection Schwantes!).

Plants compact with long shoots, isophyllous. *Leaves*: trigonous with convex sides, thick. *Capsules*: typical of genus; closing bodies sometimes smaller; covering membranes sometimes a little reduced, 6-loculed.

**65. *Antimima nordenstamii* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia nordenstamii* L.Bolus in Journal of South African Botany 30: 241 (1964). Type: *Nordenstam 799* (BOL, holo.).

Plants compact with long, erect, or decumbent shoots with dark purple to blackish internodes, several to many short shoots developing on distal nodes, arrangement resembling mistletoe on a branch, heterophyllous. *Leaves*: one leaf pair with a wide, yellow sheath with only short free parts,  $\pm 6$  mm long overall; other pair united for  $\pm 1/4$  of its length, trigonous, obtuse, up to 12 mm long; epidermis of free parts papillate. *Capsules*: typical of genus. Typical of species: blackish internodes and crowded short shoots bearing flowers.

**66. *Antimima oviformis* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia oviformis* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 261 (1931). Type: *Herre SUG9311* (BOL, holo.).

Low shrubs with long shoots only, heterophyllous. *Leaves*: sheath of one leaf pair 5–8 mm long, free papillate tips shortly triquetrous, breaking off easily leaving only sheaths on plants; other leaf pair with a short connate base, triquetrous, papillate. *Capsules*: unknown. Typical of species: bare, golden brown shoots.

**67. *Antimima papillata* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia papillata* L.Bolus in South African Gardening and Country Life 17: 256 (1927b); L.Bolus: 129 (1927/1928). *Mesembryanthemum papillatum* (L.Bolus) N.E.Br.: 32 (1930). Type: *Pillans 5713* (BOL, holo.).

*Ruschia meyeri* Schwantes: 300 (1928a). *Mesembryanthemum meyeri* (Schwantes) N.E.Br.: 32 (1930). Type: *Anon. s.n.*, photograph of type material (HBG, lecto., collection Schwantes, here designated).

Plants compact with bundles of erect long shoots, heterophyllous. *Leaves*: white, smooth sheath of one leaf

pair connate for at least  $1/2$  its length; second pair connate for  $\pm 3$  mm, free parts elongate-trigonous with rather large, dense papillae, with a dense cover of wax platelets transgrading into threads, underlying continuous wax breaking eventually into big plates. *Capsules*: without closing bodies, but with typical broad expanding keels and narrow valve wings broadest at middle, both features typical of genus.

**68. *Antimima paucifolia* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia paucifolia* L.Bolus in Journal of South African Botany 30: 240 (1964). Type: *Esterhuysen 30700* (BOL, holo.).

Shrubs with diagonal long shoots, heterophyllous. *Leaves*: sheath of one leaf pair white, basally maroon, with short free parts  $\pm 2$  mm long, upper part breaking away after resting period along pre-formed ring, leaving a clear-cut edge surrounding stem; second leaf pair triquetrous, connate part only  $\pm 1$  mm long, all free parts of leaves with papillae of medium height, keel and the margins with distant, longer papillae. *Capsules*: typical of genus. Similar to *A. exsurgens*.

**69. *Antimima pauper* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia pauper* L.Bolus in Journal of South African Botany 27: 259 (1961). Type: *Littlewood KG211/61* (BOL, holo.).

Plants compact with long shoots on which short shoots are developed in tufted bundles, isophyllous. *Leaves*: rounded at tip. *Capsules*: typical of genus.

**70. *Antimima peersii* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia peersii* L.Bolus in Notes on Mesembrianthemum and allied genera, part 1: 139 (1927/1928). *Mesembryanthemum formulosum* N.E.Br.: 32 (1930). Type: *Peers NBG3725/15* (= *BOL44507*, not 3825/15 as in one description, BOL, lecto., here designated).

Plants compact with long shoots, heterophyllous. *Leaves*: sheath of one leaf pair white, often with a copper-coloured tinge at its upper end,  $\pm 8$  mm long, free parts  $\pm 10$  mm long; subsequent leaf pair only a little connate with  $\pm 20$  mm long free parts appressed to each other during resting state, long shoots with these latter leaves only, short shoots starting with sheathed leaf pair, leaf forms alternating later; epidermis of free parts papillate. *Capsules*: typical of genus; narrow valve wings and medium-sized closing bodies.

**71. *Antimima perforata* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia perforata* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 80 (1929). *Mesembryanthemum perforatum* (L.Bolus) N.E.Br.: 32 (1930). Type: *Kolle in Pillans 6097* (BOL, lecto., here designated: chosen from several sheets).

*Ruschia paripetala* L.Bolus var. *occultans* L.Bolus: 125 (1929). Type: *Pillans 5827* (BOL, holo.).

Plants with erect, stiff branches with proleptic short shoots from a rather dense, caespitose centre. *Capsules*: typical of genus with 6 locules.



**72. *Antimima persistens* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia persistens* L.Bolus in Journal of South African Botany 29: 16 (1963) nom. illeg., non L.Bolus: 334 (1932). Type: Van Breda 1750/62 (BOL, holo.).

Plants compact with long shoots, heterophyllous. *Leaves*: sheaths of one leaf pair  $\pm 4$  mm long and free parts  $\pm 2$  mm long, these dominant on long shoots; other leaf pair connate for  $\pm 2$  mm, free parts  $\pm 4$  mm long, all free parts with elevations and papillae, on short shoots, types of leaf pairs alternating regularly, longer leaves persisting over several years. *Capsules*: typical of genus; closing bodies medium-sized.

The name *Ruschia persistens* was used for two different species by Bolus (1932, 1963), the latter being an illegitimate name in *Ruschia*. However, the epithet is available in the genus *Antimima*.

**73. *Antimima pilosula* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia pilosula* L.Bolus in Notes on Mesembryanthemum and allied genera, part 3: 259 (1954). Type: Hall NBG285/54 (BOL, holo.).

Shrubs with many scars from old leaves, isophyllous. *Leaves*: subfalcate to subclavate. *Capsules*: typical of genus; valve wings in their basal halves broader than expanding keels.

The broad, tapering valve wings, resembling those of *Eberlanzia schneideriana* (A.Berger) H.E.K.Hartmann, are unusual in the genus. The species is placed here based on the broad, typical closing bodies and the undulate covering membranes with inconspicuous closing ledges only.

**74. *Antimima piscodora* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia piscodora* L.Bolus in Notes on Mesembryanthemum and allied genera, part 1: 141 (1927/1928). *Mesembryanthemum piscodorum* (L.Bolus) N.E.Br.: 32 (1930). Type: Tugwell BOL17109 (BOL, holo.).

Plants compact with long shoots. *Capsules*: incompletely described: covering membranes touching closing body; expanding keel denticulate, but these features are typical of genus.

**75. *Antimima prolongata* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia prolongata* L.Bolus in Notes on Mesembryanthemum and allied genera, part 3: 280 (1954). Type: Acocks 16937 (sheet I) (BOL, lecto.), here designated: chosen from 2 sheets).

Plants compact with very long, thin, yellow long shoots in other bushes, heterophyllous. *Leaves*: one type of leaf pair forming a papery sheath-like cover of two parts  $\pm 10$  mm long, connate only for  $\pm 1$  mm, apical part papillate, subulate; second leaf pair  $\pm 8$ –10 mm long, triquetrous, subulate, papillate, mucro recurved. *Capsules*: typical of genus. Typical of species: pseudo-sheaths formed by one leaf pair consisting of almost free leaves, but turning papery for dry season like connate sheaths in other species.

**76. *Antimima propinqua* (N.E.Br.) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum propinquum* N.E.Br. in Kew Bulletin 1929: 59 (1929). *Ruschia propinqua* (N.E.Br.) Schwantes: 230 (1938). Type: Muir 4071 (K, holo.).

Plants compact, heterophyllous. *Leaves*: sheath of one leaf pair connate; second leaf pair almost free, 5–6 mm long, free parts keeled, margins and keel finely ciliate, all glaucous-green. *Capsules*: not known.

**77. *Antimima prostrata* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia prostrata* L.Bolus in Notes on Mesembryanthemum and allied genera, part 2: 61 (1929). *Mesembryanthemum prostratum* (L.Bolus) N.E.Br.: 32 (1930). Type: Leipoldt BOL18899 (BOL, holo.).

Plants creeping with proleptic side branches as tiny lateral bodies, later forming a mat, heterophyllous. *Leaves*: sheath of one leaf pair long, yellowish, rather smooth, enclosing larger part of subsequent leaf pair with a shorter sheath and longer free parts with papillae, in particular along margins and keel, often two or more leaf pairs of second type following each other,  $\pm 3$  mm long, body  $\pm 2.5$  mm diam. *Capsules*: typical of genus. Small-leaved version of *A. brevicarpa* sharing similar character states with that species, in particular the same type of fruit and ecology.

**78. *Antimima pumila* (Fedde & Schuster) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum pumilum* L.Bolus ex Fedde & Schuster in Just's Botanischer Jahresbericht 41: 92 (1918). *Ruschia pumila* (Fedde & Schuster) L.Bolus: 60 (1929). *Mesembryanthemum pumilum* (L.Bolus) N.E.Br.: 32 (1930) nom. illeg. Type: Pearson 3917 (BOL, holo.).

*Ruschia levynsiae* (L.Bolus) Schwantes: 58 (1949). *Mesembryanthemum levynsiae* L.Bolus: 256 (1927b). Type: Levyns NBG1373/26 (BOL, holo.).

Plants compact, heterophyllous. *Leaves*: smooth sheath on one leaf pair with short, spreading, papillate, rough tips; second leaf pair enclosed which unfolds during rainy season showing two almost oval, spreading leaves, connate slightly at bases and exhibiting upper surfaces, a rare condition in compact Ruschioideae; epidermis papillate. *Capsules*: typical of genus.

The difference in appearance between the resting state, when the yellowish green leaf pair forming a round body with the free tips protruding, and the growing phase is striking—in season, the bright green leaf pair spreads so completely that the persistent sheaths are hardly visible. This difference is the reason why Bolus described the species twice within two years, having seen *Ruschia pumila* in the resting state only, but *Ruschia levynsiae* growing, developing the described heterophylly (Figure 1E). Bolus (1913: 150) had described '*M. pumilum*, circa 5 cm altum', using the adjective as a descriptive word only, not as a formal epitheton to name a species, as she stated herself in 1929, when describing *Ruschia pumila*. Meanwhile, Fedde & Schuster (1918) had taken *Mesembryanthemum pumilum* L.Bolus as a validly described name, which it became only through their cita-

tion of the basionym and the type, hence the authorship 'L.Bolus ex Fedde & Schuster'.

**79. *Antimima pusilla* (Schwantes) H.E.K.Hartmann, comb. nov.**

*Ruschia pusilla* Schwantes in Zeitschrift für Sukkulentenkunde 3: 300 (1928a). *Mesembryanthemum parvum* N.E.Br.: 32 (1930). Type: photograph of type (HBG, lecto.), in collection Schwantes HBG, here designated).

Plants compact, heterophyllous. *Leaves*: very similar in so far as they both develop long, smooth sheaths, one leaf pair with low distant papillae on short free parts (this one persisting during dry season enclosing next leaf pair); other with distinctly longer papillae thus looking rougher, papillae elongated along margins. *Capsules*: with expanding keels merging into expanding sheets and both together covering lower half of valve (when open); closing body small with a hollow underneath into which placenta extends. The heterophylly may be overlooked easily, but the fact that during the resting time one leaf pair encloses the subsequent one indicates the different roles the two leaf pairs play.

**80. *Antimima pygmaea* (Haw.) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum pygmaeum* Haw. in Supplementum plantarum succulentarum: 98 (1819). *Ruschia pygmaea* (Haw.) Schwantes: 92 (1928b). Type: photograph no. 996/204 by Duncanson (K, lecto.), here designated).

Plants caespitose, forming mats, heterophyllous. *Leaves*: sheath of one leaf pair developing into a conical body enveloping subsequent leaf pair, upper part disintegrating into a cracked cover through which the following leaf pair grows when rain starts to fall, tips of both leaf types pointed and triangular as seen from above; epidermis very smooth, covered by a thin rugose layer of wax. *Capsules*: typical of genus; very narrow valve wings, 6-loculed. Typical of species: conical white bodies formed by leaf pairs in resting period becoming cracked with time; lacinate old leaves occur also in *A. ivori*, but those are truncate and appear like a trimmed edge.

**81. *Antimima quarzitica* (Dinter) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum quarziticum* Dinter in Feddes Repertorium 19: 151 (1923). *Ruschia quarzitica* (Dinter) Dinter & Schwantes: 69 (1929). *Corpuscularia quarzitica* (Dinter) Schwantes: 186 (1926). Type: Dinter 3866 (B, holo.).

Plants compact with erect to spreading long shoots, bearing short shoots with several leaf pairs, isophyllous. *Leaves*: triquetrous, apically recurved. *Capsules*: typical of genus; closing bodies medium-sized.

**82. *Antimima roseola* (N.E.Br.) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum roseolum* N.E.Br. in Kew Bulletin 1929: 60 (1929). *Ruschia roseola* (N.E.Br.) Schwantes: 230 (1938). Type: Muir 4067 (not 4062, as in description) (K, holo.).

Plants caespitose, heterophyllous. *Leaves*: sheath of one leaf pair long, whitish with rather short free tips; epidermis

nearly smooth; margins and keel turning white with age, keel continuing in a fold or narrow wing down sheath and stem below; second leaf pair with longer free parts with medium long papillae. *Capsules*: typical of genus; expanding tissue thick and short at base of valve, rising to inner side, but not forming a distinct expanding keel.

**83. *Antimima saturata* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia saturata* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 122 (1929). *Mesembryanthemum atrocinctum* N.E.Br.: 32 (1930). Type: Pillans BOL18952 (BOL, holo.).

Plants compact with long shoots, heterophyllous. *Leaves*: white, papery sheath of one leaf pair 3–4 mm long, free parts 4–5 mm long, with low papillae; other leaf pair united for  $\pm 2$  mm only, free parts up to 10 mm long, with long papillae on keel and margins, low papillae of different sizes on sides, wax cover dense, consisting of flakes often connected. *Capsules*: unknown.

The heterophylly had not been recognized in the original description, nor the differences in papillae. In both features, the species resembles *A. mathewsii*, which has thicker and more robust stems but is similar in the irregular branching pattern.

**84. *Antimima saxicola* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia saxicola* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 46 (1929). *Mesembryanthemum saxicola* (L.Bolus) N.E.Br.: 32 (1930). Type: Smith 4090 (sheet II) (BOL, lecto.), here designated from several sheets of that collection).

Plants compact with long shoots blackish brown with age, isophyllous. *Leaves*: triquetrous, keel and margins cartilaginous. *Capsules*: typical of genus; covering membranes deeper in centre. Plants resemble those of *Ruschia orientalis* L.Bolus and *Ruschia putterillii* (L.Bolus) L.Bolus with tiny closing bodies, in growth form and ecological preferences.

**85. *Antimima schlechteri* (Schwantes) H.E.K.Hartmann, comb. nov.**

*Ruschia schlechteri* Schwantes in Zeitschrift für Sukkulentenkunde 3: 301 (1928a). *Mesembryanthemum schlechteri* (Schwantes) N.E.Br.: 32 (1930). Type: Anon. s.n., photograph of 'type plant' (HBG, lecto.), here designated, collection Schwantes HBG).

Plants compact, with few longer shoots with dense heads of leaves and fruits, heterophyllous. *Leaves*: longer sheaths of leaf pairs persisting as a series of tubes around old stem for several years, free parts of leaves short; other type of leaf pair trigonous, epidermis almost smooth,  $\pm 9$  mm long, connate for  $\pm 5$  mm. *Capsules*: typical of genus; narrow valve wings and radial wings on covering membranes.

**86. *Antimima simulans* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia simulans* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 260 (1931). Type: Frames BOL19375 (BOL, holo.).

Low shrubs, heterophyllous. *Leaves*: sheaths of one leaf pair 4–5 mm long, free parts 1–2 mm long, papillae



low; other leaf pair with sheath  $\pm 4$  mm long, free parts up to 9 mm long, on long shoots at each node in one season. *Capsules*: unknown.

**87. *Antimima sobrina* (N.E.Br.) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum sobrinum* N.E.Br. in Kew Bulletin 1929: 60 (1929). *Ruschia sobrina* (N.E.Br.) Schwantes: 230 (1938). Type: Muir 4014 (K, holo.).

Plants caespitose, heterophyllous. *Leaves*: sheaths of one type of leaf pair connate for just over half their length; other leaf pair almost free, free parts trigonous, keel scabrous, 3–5 mm long. *Capsules*: not known.

**88. *Antimima solida* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum solidum* L.Bolus in Annals of the Bolus Herbarium 3: 136 (1922). *Ruschia solida* (L.Bolus) L.Bolus: 239 (1927b). Type: Pillans 2421 (sheet I) (BOL, lecto.), here designated: chosen from two sheets).

*Ruschia solida* (L.Bolus) L.Bolus var. *stigmatisata* L.Bolus: 94 (1929). Type: Pillans 6048 I, cited as NBG147/28, marked ' = 147/25 ' on sheet (BOL, lecto.), here designated: chosen from two sheets).

Plants compact to forming big mats, isophyllous. *Leaves*: finger-shaped to terete. *Capsules*: typical of genus; only dorsal bundles of fruit present, interior having fallen out as a tumble fruit, tiny valve wings sometimes present. Resembles *Argyroderma fissum* (Haw.) L.Bolus in its decumbent growth and finger-shaped leaves; both species grow sympatrically and can easily be confused in their vegetative state. Since fruits remain on the plants in both species, a distinction in habitat is easier.

**89. *Antimima stayneri* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia stayneri* L.Bolus in Journal of South African Botany 27: 260 (1961). Type: Stayner KG450/61 (BOL, holo.).

Shrubs with stout stems, heterophyllous. *Leaves*: papery protective cover of two parts derived from one type of leaf pair, these leaves elongate, free, to 10 mm long, tips slender, pointed, dark when dry; second pair almost free, finely papillate,  $\pm 8$  mm long. *Capsules*: typical of genus. In leaves and stems *A. stayneri* resembles *A. emarcescens* and *A. subtruncata*, but the latter species grow as climbers in other bushes.

**90. *Antimima stokoei* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia stokoei* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 160 (1929). Type: Stokoe NBG28/25 (BOL, holo.).

Plants compact, heterophyllous. *Leaves*: long sheath in one type of leaf pair, free parts with some short, dispersed papillae; other leaf pair with short sheaths and long, papillate free parts. *Capsules*: with very narrow valve wings and small closing bodies. The type looks very similar to that of *A. verruculosa*, differing mainly in the diameter of the flower, a feature known to change during anthesis.

**91. *Antimima subtruncata* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia subtruncata* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 211 (1930). Type: L.Bolus BOL19231 (BOL, holo.).

*Ruschia subtruncata* L.Bolus var. *minor* L.Bolus: 286 (1954). Type: Acocks 17185 (BOL, holo.).

Plants compact with long shoots twining in other bushes, heterophyllous; side branches with scars and somewhat spiny remains of closely set leaf pairs. *Leaves*: one leaf pair with papery protective cover of two parts  $\pm 10$  mm long, connate for only  $\pm 2$  mm, apical part papillate; second leaf pair enveloped during resting period,  $\pm 6$ –10 mm long, free parts triquetrous, papillate, with some bigger papillae along margins, mucro recurved. *Capsules*: typical of genus; expanding sheets rising to form keels. Typical of species: pseudo-sheaths formed by one leaf pair consisting of almost free leaves, but turning papery for the dry season like connate sheaths in other species; these sheaths are about as long as broad in *A. subtruncata*. Similar in general appearance to *A. emarcescens* and *A. stayneri*, both with slender leaves.

**92. *Antimima triquetra* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia triquetra* L.Bolus in South African Gardening and Country Life 18: 178 (1928a); L.Bolus: 231 (1928d). *Mesembryanthemum triquetrum* (L.Bolus) N.E.Br.: 33 (1930). Type: Banks NBG1935/15 (BOL, holo.).

Plants compact with long shoots, erect at first, later decumbent, heterophyllous. *Leaves*: one type of leaf pair with a papery protective cover of two parts  $\pm 8$  mm long, connate for only  $\pm 2$  mm, apical part subulate, with low papillae; second leaf pair  $\pm 6$ –8 mm long, triquetrous, with long papillae along keel and margins, mucro erect. *Capsules*: typical of genus. Typical of species: pseudo-sheaths formed by one leaf pair consisting of almost free leaves, but turning papery for the dry season like connate sheaths in other species—in this feature, the species resembles *A. subtruncata*.

**93. *Antimima tuberculosa* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia tuberculosa* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 110 (1929). *Mesembryanthemum enorme* N.E.Br.: 33 (1930). Type: Leipoldt BOL18940 (BOL, holo.).

Plants caespitose, forming mats with age, isophyllous. *Leaves*: trigonous. *Capsules*: typical of genus with very narrow valve wings. The epithet *tuberculosa* refers to the big closing body Bolus noticed when describing the species.

**94. *Antimima turneriana* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia turneriana* L.Bolus in Journal of South African Botany 29: 175 (1963). Type: Van Breda 1912/63 (BOL, holo.).

Plants compact in habitat, developing some long shoots in cultivation, isophyllous. *Leaves*: triquetrous with convex sides. *Capsules*: typical of genus; radial protrusions  $\pm$  wing-shaped, disintegrating later, forming rows of long teeth; valve wings at first as broad as



expanding keels, disintegrating later quickly. Similar to *A. dualis*, both compact in habitat, but the latter never changing shape.

**95. *Antimima vanzylii* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia vanzylii* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 209 (1930). Type: Van Zyl in Fuller 94 (BOL, holo.).

Plants compact with long shoots when not eaten, isophyllous. *Leaves*: triquetrous. *Capsules*: typical of genus. In spite of their strong smell of soda, plants are obviously rather heavily browsed by animals.

**96. *Antimima varians* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia varians* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 209 (1930). Type: L.Bolus BOL19212 (BOL, holo.).

Plants compact with long shoots developing shorter side shoots in bundles or groups. *Capsules*: typical of genus.

**97. *Antimima ventricosa* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum ventricosum* L.Bolus in Annals of the Bolus Herbarium 3: 128 (1922). *Cheiridopsis ventricosa* (L.Bolus) N.E.Br.: 73 (1926). *Ruschia ventricosa* (L.Bolus) Schwantes: 106 (1927). Type: Pillans NBG475/16 (BOL, holo.).

Plants compact, heterophyllous. *Leaves*: one type of leaf pair with a long sheath connate for almost half its length; second with a longer free part; free parts trigonous and papillate in both types, but more densely so in younger, less connate leaves, 40–80(–120) mm long, 13–17 mm broad, 10–13 mm diam. *Capsules*: without valve wings, expanding keels distant, 4–6-loculed, incompletely known. The low number of locules excludes the species from *Cheiridopsis*, where it might otherwise belong.

**98. *Antimima verruculosa* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia verruculosa* L.Bolus in Notes on Mesembrianthemum and allied genera, part 2: 125 (1929). *Mesembryanthemum verruculosum* (L.Bolus) N.E.Br.: 33 (1930). Type: Haynes NBG592/26 (BOL, holo.).

Low shrublets, heterophyllous. *Leaves*: sheath of one leaf pair long, smooth with a short, papillate, free part; other leaf pair with a short sheath and longer papillae. *Capsules*: with a small closing body, partly destroyed. The 'type plant' is very similar to *A. stokoei*, which has larger flowers.

**99. *Antimima watermeyerii* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Ruschia watermeyerii* L.Bolus in Notes on Mesembrianthemum and allied genera, part 1: 146 (1927/1928). Type: Watermeyer NBG554/23 (BOL, holo.).

*Ruschia stenopetala* L.Bolus: 53 (1960) Type: Littlewood KG276/60 (BOL, holo.).

*Ruschia obtusifolia* L.Bolus: 298 (1962) Type: Hall 2467 (BOL, holo.).

Plants caespitose, isophyllous. *Leaves*: trigonous to roundish. *Capsules*: typical of genus; extremely narrow valve wings at areas where expanding keel meets edge of valve.

The type material of all species included here is very similar to that of *A. klaverensis* in growth pattern, leaf shape, and fruit morphology, differing only in the absence of the fishy smell reported for the latter species.

**100. *Antimima wittebergensis* (L.Bolus) H.E.K.Hartmann, comb. nov.**

*Mesembryanthemum wittebergense* L.Bolus in Annals of the Bolus Herbarium 4: 88 (1927a). *Ruschia wittebergensis* (L.Bolus) Schwantes: 106 (1927). Type: Compton NBG 1920/24 (BOL, holo.).

Plants caespitose, isophyllous. *Leaves*: cymbiform or boat-shaped. *Capsules*: with small closing bodies, exceptionally broad and thick closing ledges and narrow valve wings.

**SPECIES EXCLUDED FROM *ANTIMIMA***

***Ruschia virgata* (Haw.) L.Bolus in South African Gardening and Country Life 17: 239 (1927); L.Bolus: 72 (1927/1928).**

*Mesembryanthemum virgatum* Haw.: 88 (1803); *Antimima virgata* (Haw.) Dehn: 213 (1989). Type: Bortenschlag s.n. (K, lecto.), designated by Dehn 1989: 213).

Plants with erect, thin branches from a denser centre, often in other bushes. *Leaves*: triquetrous, hardly connate, pair at its base leaving a triangle of stem visible between them. *Capsule*: base elongate, funnel- to bell-shaped, top almost semi-orbicular from high valve rims; covering membranes forming a roof, ridge being the contact line, closing ledges sharp and long; closing body nearly hook-shaped, hollow; expanding keels distant at bases. Material matching the collection of Bortenschlag, which was seen by Haworth, possesses fruits of the *Ruschia* type, with deep locules and small, hook-shaped closing bodies. The species is therefore placed back in *Ruschia*.

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# Meiotic chromosome behaviour in *Cenchrus ciliaris* (Poaceae: Panicoideae)

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**Keywords:** *Cenchrus ciliaris*, chromosomes, meiosis, Panicoideae, Poaceae, polyploidy

## ABSTRACT

A basic chromosome number of  $x = 9$  has been confirmed for *Cenchrus ciliaris* L. Polyploidy is common and levels vary from tetraploid to hexaploid. Aneuploidy is reported for a single specimen, where two chromosomes of a single genome were lost. Various meiotic irregularities were observed. The highest incidence of meiotic abnormalities was observed in the pentaploid specimens. This was attributed to their uneven polyploid level. All specimens varied from segmental allopolyploid to allopolyploid.

## INTRODUCTION

The classification of the genus *Cenchrus* L. is complex (De Lisle 1963) and it is sometimes difficult to describe species on gross morphological characters alone (Chapman 1990). Meiotic chromosome behaviour can make a vast contribution to the classification process.

The aim of the present study was to use meiotic chromosome behaviour in *C. ciliaris* in order to deduce the polyploid origin of the specimens studied, as well as the chromosomal variation within and among populations of *C. ciliaris* in South Africa.

## MATERIALS AND METHODS

Specimens were collected and fixed in the veld. Voucher herbarium specimens are housed in the Geo Potts Herbarium, Department of Botany and Genetics, University of the Orange Free State, Bloemfontein (BLFU) (Table 1).

Slides were prepared for meiotic analysis (Visser & Spies 1994). A minimum of 20 cells of each of the following stadia were studied: diakinesis, metaphases I and II, anaphases I and II and telophases I and II. The following were recorded: gametic chromosome numbers, the number of univalents, laggards and micronuclei during metaphase I, anaphase I and II, and telophase I and II, respectively. The number of chiasmata per cell was inferred from the chromosome configurations observed during diakinesis or metaphase I.

The genomic constitution of some of the tetraploid plants was calculated, based on the models proposed by Kimber & Alonso (1981). Expected chromosome configurations for each of the proposed models (4:0, 3:1, 2:1:1 and 2:2) were calculated and compared with those observed. The average sum of squares (SS) between the expected and the observed values were calculated. The

relative affinity between the pairs of genomes was expressed as an  $x$ -value. An  $x$ -value of 0.5 indicated a close affinity between corresponding (homologous) genomes, whereas non-homologous genomes were represented by an  $x$ -value of 1. The model with the lowest SS-value provided the best 'fit' for that particular specimen. The specific model was then considered to represent the genomic constitution of the specimen.

## RESULTS

From all the meiotic stages studied, only metaphase I, anaphase I and telophase I, proved to contribute to meiotic analyses. Four ploidy levels, namely aneuploidy ( $n = 2x - 1 = 17$ ), tetraploidy ( $n = 2x = 18$ ), pentaploidy ( $n = 5/2x = 45/2$ ) and hexaploidy ( $n = 3x = 27$ ) were observed, based on a basic chromosome number of  $x = 9$  (Table 2).

A wide range of meiotic abnormalities were observed for *Cenchrus ciliaris*. These abnormalities included the presence of univalents during metaphase I, chromosome and chromatid laggards during anaphases I and II respectively, uneven segregation of chromosomes during anaphase I, anaphase I bridges and micronuclei during telophases I and II. Two additional meiotic abnormalities were observed, namely precocious disjunction of chromosomes into chromatids during anaphase I and the absence of cytokinesis at the end of telophase I.

The presence of univalents, chromosome and/or chromatid laggards and micronuclei, were compared among the tetraploid specimens. A histogram was plotted, based on the percentage of cells containing the various numbers of univalents, chromosome and/or chromatid laggards and micronuclei (Figure 1). The topography of the curves corresponded. This fact indicated that, for *C. ciliaris*, the number of univalents present during metaphase I, is the most likely reason why there is an increase in the chromosome and/or chromatid laggards observed during anaphase I. This in turn, could have contributed to the formation of micronuclei during telophase I. The absence of various peaks in the hyperboles indicates that no distinct chromosomal groups exist in the tetraploid specimens. Therefore, the average percentages for each

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TABLE 1.—List of *Cenchrus ciliaris* specimens studied, voucher specimen numbers and localities according to the degree reference system (Edwards & Leistner 1971)

n	Locality	Voucher
17	NORTH-WEST.—2627 (Potchefstroom): in Potchefstroom, on route to Orkney, (–CA)	<i>Spies 5883</i>
18	GAUTENG.—2528 (Pretoria): near Pretoria, (–CC)	<i>Spies 5645</i>
	NORTH-WEST.—2627 (Potchefstroom): in Potchefstroom, on route to Orkney, (–CA)	<i>Spies 5653, 5654</i>
	GAUTENG.—2628 (Johannesburg): Grassmere Garage, Johannesburg, (–AB)	<i>Spies 5646</i>
	NORTH-WEST.—2724 (Taung): 101 km from Kuruman to Vryburg, (–AB)	<i>Spies 5527</i>
	NORTH-WEST.—2725 (Bloemhof): in Amalia, on route to Schweizer-Reneke, (–AA)	<i>Spies 5538</i>
	NORTH-WEST.—2725 (Bloemhof): 2 km from Britten to Christiana, (–CB)	<i>Spies 5542, 5543</i>
	FREE STATE.—2726 (Odendaalsrus): 8 km from Wesselsbron to Bultfontein, (–CD)	<i>Spies 5659</i>
	FREE STATE.—2726 (Odendaalsrus): 46 km from Bothaville to Wesselsbron, (–DA)	<i>Spies 5657</i>
	FREE STATE.—2727 (Kroonstad): 61 km from Kroonstad to Parys, (–AC)	<i>Spies 5650</i>
	FREE STATE.—2727 (Kroonstad): 7 km from Kroonstad to Kroonvaal, (–CA)	<i>Spies 5649</i>
	KWAZULU-NATAL.—2732 (Ubombo): Mhlosinga, on route to Sordwana, (–CC)	<i>Venter 9286</i>
	NORTHERN CAPE.—2822 (Glen Lyon): 7 km from Smidtsdrift to Postmasburg, (–DA)	<i>Spies 5521</i>
	FREE STATE.—2826 (Brandfort): 57 km from Wesselsbron to Bultfontein, (–AA)	<i>Spies 5662</i>
	FREE STATE.—2826 (Brandfort): 30 km from Wesselsbron to Bultfontein, (–BB)	<i>Spies 5660</i>
	FREE STATE.—2826 (Brandfort): 25 km from Bloemfontein to Brandfort, (–CD)	<i>Spies 5576, 5577</i>
	FREE STATE.—2826 (Brandfort): 27 km from Bloemfontein to Brandfort, (–CD)	<i>Spies 5574, 5575</i>
	FREE STATE.—2826 (Brandfort): 38 km from Bloemfontein to Brandfort, (–CD)	<i>Spies 5849, 5850</i>
	FREE STATE.—2826 (Brandfort): 32 km from Bloemfontein to Abrahamskraal, (–CD)	<i>Spies 5638</i>
	FREE STATE.—2925 (Jagersfontein): 44 km from Petrusburg to Kimberley, (–AB)	<i>Spies 5508</i>
	FREE STATE.—2926 (Bloemfontein): near Bloemfontein, (–AA)	<i>Spies 5643, 5664</i>
	FREE STATE.—2926 (Bloemfontein): 16 km from Bloemfontein to Winburg, (–AA)	<i>Spies 5847</i>
	EASTERN CAPE.—3125 (Steynsburg): 30 km from Steynsburg to Hofmeyr, (–BC)	<i>Spies 5669</i>
	EASTERN CAPE.—3125 (Steynsburg): near Hofmeyr, (–DC)	<i>Spies 5587</i>
	EASTERN CAPE.—3125 (Steynsburg): 12 km from Hofmeyr to Cradock, (–DC)	<i>Spies 5670</i>
	WESTERN CAPE.—3222 (Beaufort West): 5 km from Beaufort West, (–BC)	<i>Spies 5487, 5489</i>
	EASTERN CAPE.—3224 (Graaff-Reinet): 58 km from Jansenville to Graaff-Reinet, (–BC)	<i>Spies 5240</i>
	EASTERN CAPE.—3224 (Graaff-Reinet): 131 km from Uitenhage to Graaff-Reinet, (–DC)	<i>Spies 5236</i>
	EASTERN CAPE.—3224 (Graaff-Reinet): 145 km from Uitenhage to Graaff-Reinet, (–DC)	<i>Spies 5237</i>
	EASTERN CAPE.—3224 (Graaff-Reinet): 122 km from Patensie to Willowmore, (–DD)	<i>Spies 5215</i>
	EASTERN CAPE.—3225 (Somerset East): 57 km from Cradock to Cookhouse, (–DB)	<i>Spies 5591</i>
	EASTERN CAPE.—3225 (Somerset East): Koksraal, Cookhouse, (–DB)	<i>Spies 5594, 5676</i>
	WESTERN CAPE.—3320 (Ladismith): 4 km from Calitzdorp to Oudtshoorn via Kuilsrivier, (–DC)	<i>Spies 5226</i>
	EASTERN CAPE.—3324 (Steytlerville): 102 km from Uitenhage to Graaff-Reinet, (–BD)	<i>Spies 5232</i>
	EASTERN CAPE.—3324 (Port Elizabeth): 40 km from Uitenhage to Graaff-Reinet, (–CD)	<i>Spies 5230</i>
18+0-2B	NORTH-WEST.—2624 (Vryburg): near Vryburg, on route to Kuruman, (–DC)	<i>Spies 5531</i>
	NORTH-WEST.—2627 (Potchefstroom): 10 km from Parys to Potchefstroom, (–CD)	<i>Spies 5652</i>
	FREE STATE.—2925 (Jagersfontein): 60 km from Petrusburg to Kimberley, (–AA)	<i>Spies 5512</i>
	FREE STATE.—2926 (Bloemfontein): 25 km from Bloemfontein to Winburg, (–AA)	<i>Spies 5848</i>
	EASTERN CAPE.—3125 (Steynsburg): 10 km from Steynsburg to Hofmeyr, (–BC)	<i>Spies 5584, 5585</i>
	EASTERN CAPE.—3125 (Steynsburg): 24 km from Steynsburg to Hofmeyr, (–BC)	<i>Spies 5586</i>
	WESTERN CAPE.—3222 (Beaufort West): 5 km from Beaufort West, (–BC)	<i>Spies 5488</i>
	EASTERN CAPE.—3225 (Somerset East): Koksraal, Cookhouse, (–DB)	<i>Spies 5675</i>
	EASTERN CAPE.—3324 (Steytlerville): 68 km from Uitenhage to Graaff-Reinet, (–DA)	<i>Spies 5231</i>
	EASTERN CAPE.—3325 (Port Elizabeth): 30 km from Uitenhage to Graaff-Reinet, (–CD)	<i>Spies 5229</i>
45/2	NORTH-WEST.—2522 (Sanie): in the riverbed at Watersend, (–DB)	<i>Spies 5497</i>
	FREE STATE.—2925 (Jagersfontein): Spitskop farmyard, Fauresmith, (–DA)	<i>Du Preez 2758</i>
	NORTHERN CAPE.—3024 (Colesberg): 27 km from Verwoerddain to Venterstad, (–DA)	<i>Spies 5581, 5583</i>
	EASTERN CAPE.—3224 (Graaff-Reinet): 39 km from Jansenville to Graaff-Reinet, (–DA)	<i>Spies 5239</i>
	EASTERN CAPE.—3224 (Graaff-Reinet): 15 km from Jansenville to Graaff-Reinet, (–DC)	<i>Spies 5238</i>
	EASTERN CAPE.—3224 (Graaff-Reinet): 76 km from Patensie to Willowmore, (–DD)	<i>Spies 5210</i>
27	NORTHERN CAPE.—2824 (Kimberley): 1 km from Kimberley to Griekwastad, (–DA)	<i>Spies 5513, 5514</i>
	FREE STATE.—2925 (Jagersfontein): 44 km from Petrusburg to Kimberley, (–AB)	<i>Spies 5510</i>
27+0-1B	NORTHERN CAPE.—2824 (Kimberley): 1 km from Kimberley to Griekwastad, (–DA)	<i>Spies 5517</i>

TABLE 2.—Meiotic chromosome behaviour of *Cenchrus ciliaris* specimens showing voucher specimen no.; gametic chromosome no. (n); average frequency of univalents (l); frequency of chromosome laggards; percentage of cells studied containing anaphase I bridges; frequency of micronuclei during telophase I. All ranges are included in brackets

Voucher no.	n	l	# laggards	% bridges	# micronuclei
<i>Spies 5883</i>	17	1.5 (0–4)	2.9 (0–8)	20	0.9 (0–2)
<i>Spies 5215</i>	18	-	3.2 (0–6)	0	3.8 (0–8)
<i>Spies 5226</i>	18	0.3	-	0	1.0 (0–2)
<i>Spies 5229</i>	18	2.0 (1–3)	4.0 (0–6)	0	3.2 (0–8)
<i>Spies 5230</i>	18	5.1 (0–18)	2.9 (0–12)	6.3	2.7 (0–5)
<i>Spies 5231</i>	18	1.2 (0–2)	4.6 (0–9)	9.1	1.3 (0–4)
<i>Spies 5232</i>	18	3.2 (0–10)	2.0 (0–6)	9.1	3.0 (0–5)
<i>Spies 5236</i>	18	0.6 (0–4)	2.2 (0–6)	9	1.1 (0–5)
<i>Spies 5237</i>	18	1.5 (0–3)	3.9 (0–8)	6.3	1.9 (0–6)
<i>Spies 5240</i>	18	6.5 (0–8)	8.8 (0–16)	0	1.1 (0–5)
<i>Spies 5487</i>	18	0.5 (0–2)	1.1 (0–5)	30	0
<i>Spies 5488</i>	18	0.6 (0–2)	0.8 (0–2)	33.3	0.5 (0–2)
<i>Spies 5489</i>	18	0	4.0 (0–6)	-	0.4 (0–1)
<i>Spies 5508</i>	18	2.3 (0–5)	1.4 (0–5)	0	1.8 (0–5)
<i>Spies 5509</i>	18	-	-	-	-
<i>Spies 5512</i>	18	2.0 (0–6)	4.1 (0–9)	7.1	2.4 (0–5)
<i>Spies 5521</i>	18	2.7 (0–6)	1.3 (0–5)	15.4	2.9 (0–9)
<i>Spies 5522</i>	18	-	-	-	-
<i>Spies 5525</i>	18	2.0 (0–4)	-	-	0.2 (0–1)
<i>Spies 5527</i>	18	-	0	0	0.9 (0–2)
<i>Spies 5529</i>	18	-	4.2 (1–8)	0	0
<i>Spies 5531</i>	18	2.8 (0–6)	1.3 (0–5)	0	0.5 (0–4)
<i>Spies 5538</i>	18	-	0.2 (0–2)	0	0.2 (0–1)
<i>Spies 5539</i>	18	-	-	-	-
<i>Spies 5542</i>	18	1.4 (0–5)	2.2 (0–5)	10	3.3 (1–7)
<i>Spies 5543</i>	18	2.7 (1–4)	4.0	-	0.7
<i>Spies 5553</i>	18	-	-	-	-
<i>Spies 5574</i>	18	0.4 (0–1)	0.3 (0–1)	0	0.7 (0–3)
<i>Spies 5575</i>	18	1.6 (0–4)	0.5 (0–10)	8.3	0.7 (0–3)
<i>Spies 5576</i>	18	-	0.7 (0–3)	0	0.8 (0–4)
<i>Spies 5577</i>	18	-	1.0 (0–3)	0	1.0 (0–4)
<i>Spies 5584</i>	18	2.3 (0–8)	1.5 (0–6)	14.3	0.1 (0–1)
<i>Spies 5585</i>	18	0.6 (0–2)	0	0	1.0 (0–3)
<i>Spies 5586</i>	18	0.7 (1)	0.8 (0–2)	0	1.1 (0–3)
<i>Spies 5587</i>	18	-	0	0	0.2 (0–1)
<i>Spies 5591</i>	18	-	1.9 (0–5)	27.2	1.2 (0–3)
<i>Spies 5594</i>	18	-	1.7 (0–5)	30	2.1 (1–5)
<i>Spies 5638</i>	18	1.7 (0–4)	2.8 (0–5)	0	1.0 (0–6)
<i>Spies 5642</i>	18	-	-	-	-
<i>Spies 5643</i>	18	-	4.0 (0–6)	0	3.0 (0–3)
<i>Spies 5645</i>	18	2.3 (0–8)	1.5 (0–3)	-	1.0 (0–3)
<i>Spies 5646</i>	18	-	0	12.5	1.6 (0–1)
<i>Spies 5649</i>	18	2.5 (0–8)	0.4 (0–3)	0	1.1 (0–1)
<i>Spies 5650</i>	18	2.7 (1–4)	0.9 (0–10)	10	0.4 (0–2)
<i>Spies 5652</i>	18	1.9 (0–4)	1.2 (0–5)	71.4	3.3 (2–6)
<i>Spies 5653</i>	18	2.3 (0–5)	0	0	0.5 (0–2)
<i>Spies 5654</i>	18	0.7 (0–3)	0	0	1.5 (0–4)
<i>Spies 5655</i>	18	-	0.3 (0–1)	20	0.9 (0–4)
<i>Spies 5657</i>	18	-	0	0	0.4 (0–1)
<i>Spies 5659</i>	18	1.4 (0–4)	0.2 (0–1)	10	0.1 (0–1)
<i>Spies 5660</i>	18	1.8 (0–4)	0	10	0.5 (0–2)
<i>Spies 5662</i>	18	-	0.9 (0–6)	0	1.0 (0–3)
<i>Spies 5664</i>	18	2.4 (0–5)	1.5 (0–6)	0	0.4 (0–2)
<i>Spies 5668</i>	18	-	-	-	-
<i>Spies 5669</i>	18	3.3 (1–4)	0.3 (0–1)	0	0.4 (0–2)
<i>Spies 5670</i>	18	0.2 (0–1)	1.5 (0–5)	0	0.5 (0–3)
<i>Spies 5671</i>	18	-	-	-	-
<i>Spies 5675</i>	18	-	-	-	1.5 (0–5)
<i>Spies 5676</i>	18	-	3.4 (0–5)	0	1.6 (0–6)
<i>Spies 5847</i>	18	1.4 (0–4)	0	-	0.4 (0–2)
<i>Spies 5848</i>	18	2.8 (0–4)	0	16.7	0.6 (0–2)
<i>Spies 5849</i>	18	-	-	-	0.8 (0–3)
<i>Spies 5850</i>	18	1.4 (0–3)	1.4 (0–2)	11.1	0.7 (0–4)
<i>Venter 9286</i>	18	1.8 (0–4)	3.1 (0–10)	30	1.8 (0–4)
Average		1.9	1.7	8.3	1.1
<i>Du Preez 2758</i>	45/2	4.0 (3–9)	8.2 (7–12)	0	3.5 (2–5)
<i>Spies 5210</i>	45/2	4.6 (3–8)	11.6 (7–14)	0	4.8 (0–11)
<i>Spies 5238</i>	45/2	4.8 (1–10)	7.1 (1–18)	0	2.3 (0–7)
<i>Spies 5239</i>	45/2	3.5 (2–8)	11.8 (1–20)	0	4.0 (1–5)
<i>Spies 5497</i>	45/2	3.4 (2–4)	3.0 (0–6)	0	3.6 (0–5)
<i>Spies 5581</i>	45/2	-	10.7 (1–32)	0	4.6 (2–9)
<i>Spies 5583</i>	45/2	4.0 (2–9)	10.0 (1–20)	0	6.2 (1–10)
Average		4.0	9.2	0	4.1

TABLE 2. (cont.)—Meiotic chromosome behaviour of *Cenchrus ciliaris* specimens showing voucher specimen no.; gametic chromosome no. (n); average frequency of univalents (I); frequency of chromosome laggards; percentage of cells studied containing anaphase I bridges; frequency of micronuclei during telophase I. All ranges are included in brackets

Voucher no.	n	I	# laggards	% bridges	# micronuclei
<i>Spies 5510</i>	27	4.1 (2–7)	2.5 (0–8)	0	2.8 (0–8)
<i>Spies 5513</i>	27	-	2.0 (0–4)	0	4.8 (0–8)
<i>Spies 5514</i>	27	2.5 (0–8)	6.1 (1–9)	24.3	4.5 (0–8)
<i>Spies 5515</i>	27	1.8 (0–5)	2.4 (0–5)	10	3.1 (0–6)
<i>Spies 5517</i>	27	1.3 (0–3)	5.2 (0–20)	0	2.2 (0–6)
Average		2.8	3.3	6.9	3.8

-, cells in the particular meiotic stage have not been observed, or a complete meiotic analysis (involving at least 10 cells of the particular stage) could not be concluded.

of the three chromosome abnormalities will be representative of all the tetraploid specimens. This process was not repeated for the pentaploid and hexaploid specimens, due to the limited number of specimens available.

The average numbers of univalents observed in the specimens investigated were 1.5, 1.9, 4.0 and 2.8 respectively for the n = 17, n = 18, n = 45/2, and n = 27 specimens. The variation in the number of univalents is indicated in Table 2. The highest number of univalents (0–18) was observed for *Spies 5230* (n = 18) (Figure 2B, C).

The univalents present were usually situated near the equator (Figure 2A–D) and moved onto the plate where they orientated themselves both syntelically and amphitelically. This led to the centromeres of the two chromatids either undergoing reductional distribution or equational distribution. The chromatids segregated to opposite poles.

Since the B-chromosomes were mostly indistinguishable from the normal euchromosome complement, specimens containing B-chromosomes were excluded during the calculation of the univalent, laggard and micronuclei averages.

Chromosome and chromatid laggards were frequently observed during anaphase I (Figure 3A–E). The average

numbers of chromosome laggards observed, were 2.9, 1.7, 9.2 and 3.3 for the n = 17, n = 18, n = 45/2, and n = 27 specimens, respectively (Table 2). The variation in numbers is indicated in Table 2. The highest number of laggards (1–32) was observed for *Spies 5581* (n = 45/2).

The number of micronuclei observed during telophase I varied (Figure 4A–D). The average numbers of micronuclei observed were 0.9 (n = 17), 1.1 (n = 18), 4.1 (n = 45/2) and 3.8 (n = 27) (Table 2). The variation in numbers is indicated in Table 2. The highest number of micronuclei (11) was observed for *Spies 5210* (n = 45/2) (Figure 4B). The size of these micronuclei varied (Figure 4B, D).

Genome interpretation was performed on three tetraploid specimens (*Spies 5215*, *5240* and *5649*). These analyses revealed that the 2:2 model (Kimber & Alonso 1981) fitted the specimens to the greatest degree, with x-values of 1 or approximately 1 (Table 3).

Anaphase bridges were observed in 26 specimens of *C. ciliaris* (Table 2) (Figure 5A–C). The average number of cells per specimen which contained bridges, varied from nought to a maximum of 71.4% (*Spies 5652*) (Table 2). The acentric fragment could most often be observed (Figure 5A, B), and varied in size among the various specimens.

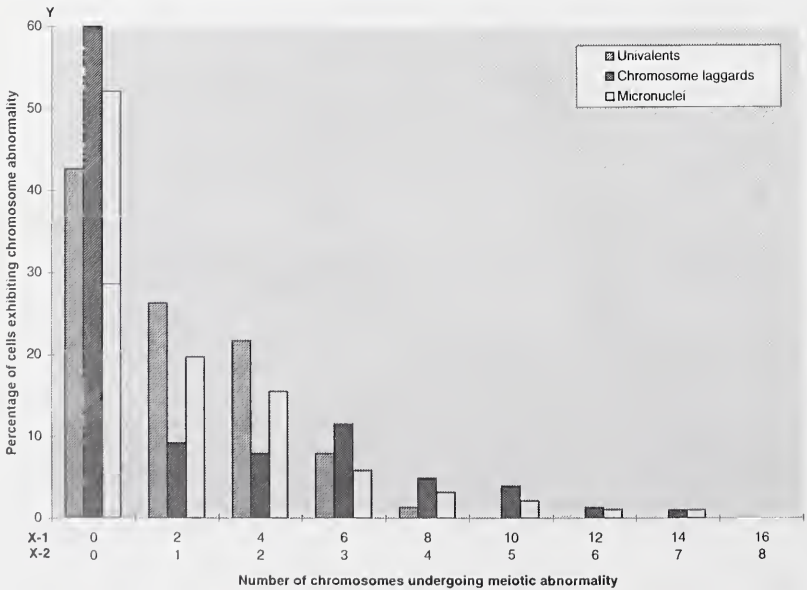


FIGURE 1.—Histogram, indicating percentage of tetraploid cells exhibiting univalents during metaphase I, chromosome laggards during anaphase I, and micronuclei during telophase I. X-1, number of chromosomes involved in formation of univalents and chromosome laggards; X-2, number of micronuclei observed per cell.



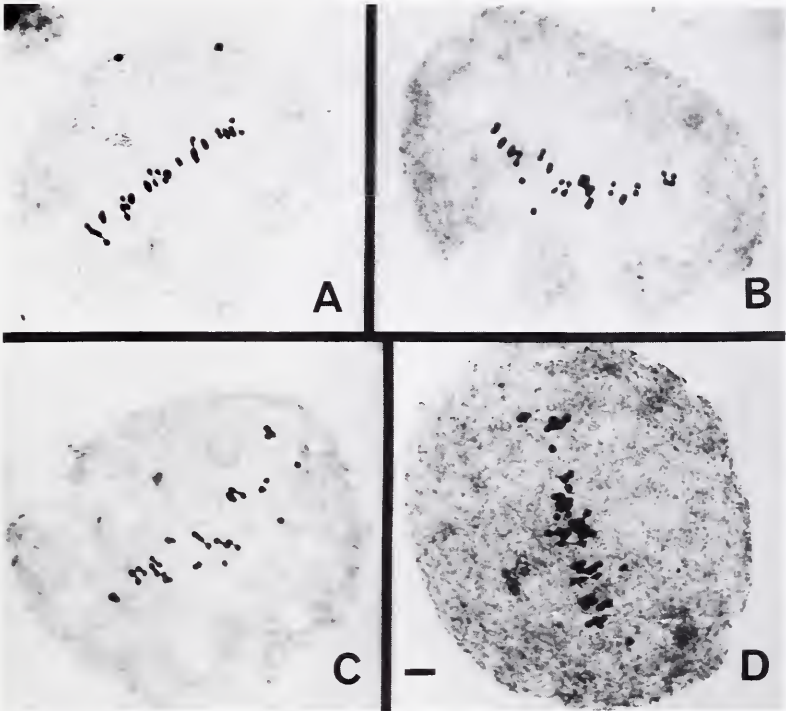


FIGURE 2.—Variation in number of univalents observed during metaphase I in *Cenchrus ciliaris*. A, *Spies* 5240,  $n = 2x = 18$ , with two univalents; B, *Spies* 5230,  $n = 2x = 18$ , with two univalents; C, *Spies* 5230,  $n = 2x = 18$ , with eight univalents; D, *Spies* 5514,  $n = 3x = 27$ , with numerous univalents. Scale bar: 10  $\mu$ m.

DISCUSSION

Basic chromosome numbers constitute the core of any meiotic study, as they are essential for confirming the presence of polyploidy. *Cenchrus ciliaris* has a basic chromosome number of  $x = 9$  and polyploidy is present. Three polyploid levels have been observed, with the most abundant being the tetraploids (82.9%). The penta-

and hexaploids were observed at much lower frequencies (9.2% and 6.6% respectively).

Polyploidy is prominent in the plant kingdom (Stebbins 1982). Polyploid levels for *C. ciliaris*, taking the published aneuploid chromosome numbers into account, include diploidy, triploidy, tetraploidy, pentaploidy, hexaploidy and nanopolyploidy. References for these

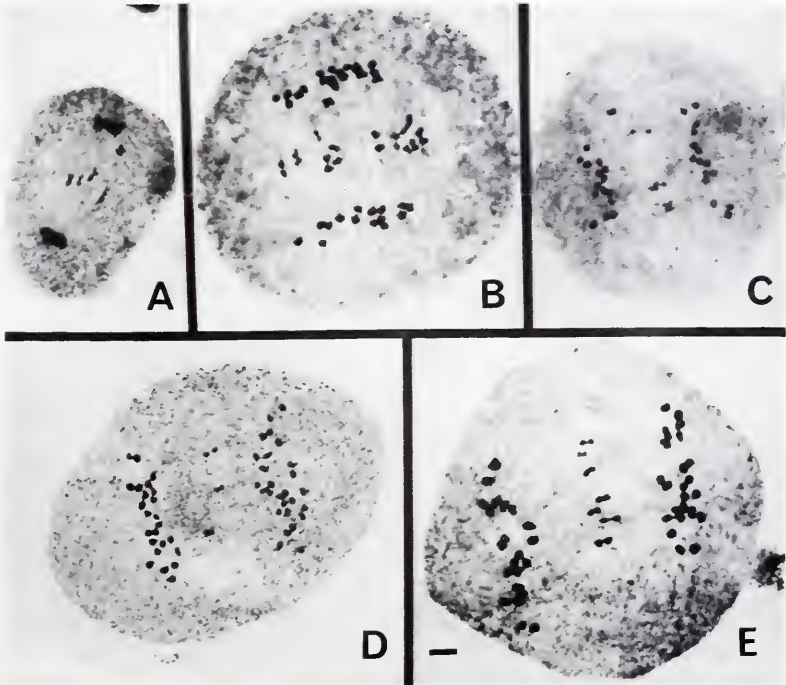


FIGURE 3.—Variation in number of chromosome and chromatid laggards observed during anaphase I in *Cenchrus ciliaris*. A, *Spies* 5883,  $n = 17$ ; B, *Spies* 5508,  $n = 2x = 18$ ; C, *Spies* 5583,  $n = 5/2x = 45/2$ ; D, *Spies* 5514,  $n = 3x = 27$ ; E, *Spies* 5514,  $n = 3x = 27$ . Scale bar: 10  $\mu$ m.

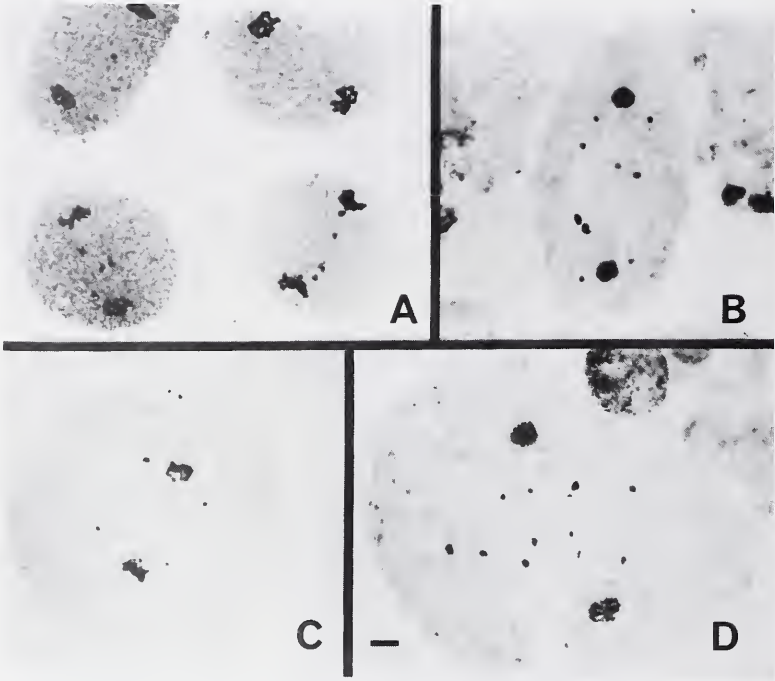


FIGURE 4.—Variation in number and size of micronuclei observed during telophase I and II in *Cenchrus ciliaris*. A, *Spies 5542*,  $n = 2x = 18$ , telophase II, with 0–4 per cell; B, *Spies 5210*,  $n = 5/2x = 45/2$ , telophase I, with nine micronuclei; C, *Spies 5583*,  $n = 5/2x = 45/2$ , telophase I, with minimum of four micronuclei; D, *Spies 5514*,  $n = 3x = 27$ , telophase I, with 10 micronuclei. Scale bar: 10  $\mu$ m.

chromosome numbers are presented in Visser *et al.* (in prep.). The wide range of polyploid levels and very low frequency of diploids indicate that this species forms a mature polyploid complex.

The meiotic chromosome behaviour of the polyploid specimens varied from being normal to highly irregular, depending on the number of genomes present and their homology. Polyploids with an even number of genomes are influenced less dramatically during meiosis than those with an uneven number of genomes. Uneven polyploid levels have more meiotic abnormalities, due to the presence of an uneven number of sets of chromosomes which complicates chromosome pairing. Genome homology also plays an important role in the normality of meiosis. It can affect chromosome pairing to such an extent that from univalents to multivalents are formed.

In order to attest the proposed basic chromosome number of  $x = 9$  for *C. ciliaris*, a comparison was made between the observed and the expected meiotic chromosome behaviour of each of the polyploid levels studied. The presence of univalents during metaphase I was reg-

ularly observed. A variation in the number of univalents present occurred within and among the polyploid levels (Figure 2A–D). The highest average numbers of univalents were observed in the pentaploid specimens (4.0), whereas for the hexaploid specimens, they were 2.8 (Table 2). Approximately similar average numbers of univalents were observed for the aneuploid and tetraploid specimens (1.5 versus 1.9).

The increased averages of univalents present during metaphase I for the pentaploids and the hexaploids were expected, as a higher incidence of meiotic irregularities is closely associated with uneven and higher polyploid levels (Stebbins 1950). The variation in the number of univalents observed within each of these polyploid levels, indicates chromosomal differences among the specimens.

The number of univalents present during metaphase I corresponds with the numbers of chromosome laggards and micronuclei observed (Figure 1). The data suggest that the univalents observed during metaphase I were mostly lagging during anaphase I (Figure 3A–E), and led

TABLE 3.—Genomic constitution of tetraploid *Cenchrus ciliaris* specimens, according to models of Kimber & Alonso (1981): voucher nos, chiasma frequencies, relative x-values and the appropriate average sum of squares for each of the various models in brackets (M)

Voucher	Chiasma frequency	M			
		4:0	3:1	2:2	2:1:1
<i>Spies 5215</i>	1.3	- (16.778)	0.889 (21.192)	1 (8.429)	0.828 (16.18)
<i>Spies 5240</i>	1.2	- (14.026)	8.874 (17.866)	1 (3.564)	0.872 (12.801)
<i>Spies 5649</i>	1.4	- (9.876)	0 (14.324)	0.84 (4.465)	0.632 (8.03)

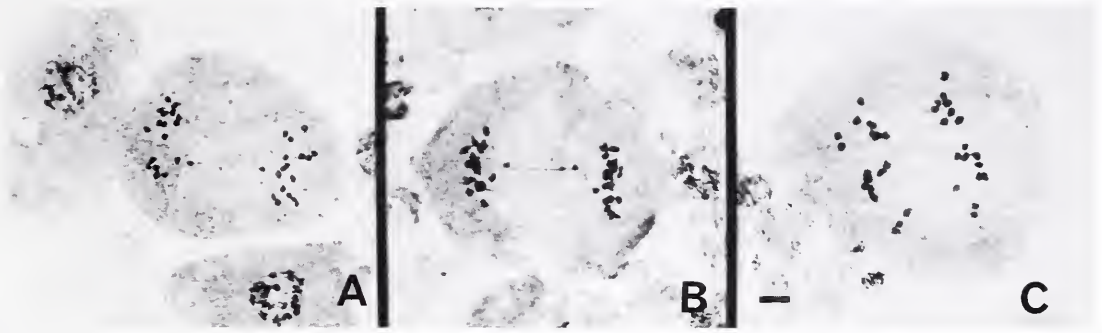


FIGURE 5.—Some anaphase I bridges observed in *Cenchrus ciliaris*. A, *Spies* 5652,  $n = 2x = 18$ ; B, *Spies* 5594,  $n = 2x = 18$ ; C, *Spies* 5574,  $n = 2x = 18$ . Scale bar: 10  $\mu$ m.

to the formation of micronuclei during telophase I. The average number of laggards was the highest for the pentaploid specimens (9.2 laggards per cell), followed by the hexaploid and aneuploid specimens (3.3 and 2.9 respectively) (Table 2). The number of chromosome and chromatid laggards varied among the specimens of the various polyploid levels, emphasizing genetic differences among specimens within each of the polyploid levels.

The average number of micronuclei also varied among the specimens of each polyploid level (Table 2). The micronuclei were not incorporated into the daughter nuclei at the time of cell division (Figure 4A–D). The highest average number was observed in the pentaploid specimens (4.1), followed by the hexaploid (3.8), tetraploid (1.1) and aneuploid (0.9) specimens respectively. The highest number and greatest variation of micronuclei were observed in the pentaploid specimens (Figure 4B, C) (Table 2).

The highest average numbers of univalents, chromosome laggards and micronuclei have been observed in the pentaploid specimens (Table 2). This polyploid level was followed by the hexaploids, whereas for the tetraploids and the single aneuploid specimen, the level was approximately similar. The high incidence of meiotic abnormalities in the pentaploid specimens was expected, due to their uneven polyploid levels. An average number of 9.2 chromosomes lagged during anaphase I and was representative of an entire genome. A basic chromosome number of  $x = 9$  for *C. ciliaris*, due to the presence of a fifth genome lagging during anaphase I, is hereby confirmed.

Genome variation in the tetraploid specimens was confirmed during this study. Meiosis was normal in some specimens (*Spies* 5522), whereas for others, it was highly irregular (*Spies* 5230) (Table 2). The average numbers of univalents present and chromosome laggards observed, were almost similar (1.9 and 1.7, respectively). These averages suggest two univalents observed during metaphase I, lagging during anaphase I, and finally forming a single micronucleus (1.1 per cell) (Table 2).

Genome interpretation of three tetraploid specimens (*Spies* 5215, 5240 & 5649) revealed that the 2:2 model (Kimber & Alonso 1981) agreed best with these specimens, with  $x$ -values of 1 (*Spies* 5215 & 5240) and 0.84 (*Spies* 5649) (Table 3). An  $x$ -value of 1 inferred two dis-

tinctly different sets of genomes, therefore, *Spies* 5215 and 5240 were classified as allotetraploids (for example AABB). Although the 2:2 model fitted *Spies* 5649 the best, a lower  $x$ -value of 0.84 was calculated (Table 3). This specimen was classified as a segmental allopolyploid, based on the lower  $x$ -value and the occasional presence of quadrivalents (for example AAA'A').

The specimens' genomic constitutions were attested by their meiotic chromosome behaviour. The specimens differed in respect of their meiotic behaviour. Quadrivalents were observed in *Spies* 5215 and 5649, whereas for *Spies* 5240, univalents and bivalents were observed. The number of quadrivalents observed in the two specimens varied. One to three quadrivalents were observed for *Spies* 5649, whereas for *Spies* 5215, an infrequent quadrivalent was observed.

*Spies* 5240 was confirmed as an allopolyploid (for example AABB), based on the presence of bivalents only, observed during metaphase I. The presence of an occasional quadrivalent in cells of *Spies* 5215 and one to three quadrivalents per cell in *Spies* 5649, justify segmental allopolyploidy (for example AAA'A') for both these specimens. However, the presence of genes, controlling homoeologous chromosome pairing in *Cenchrus*, should be studied before these genomic constitutions can be accepted.

The two allopolyploid specimens were collected in the Eastern Cape, whereas *Spies* 5649 was collected in the Free State (Table 1). Taking their different geographical localities into consideration, it is suggested that the Eastern Cape specimens represent a genetically different group (or hybrid swarm) from those in the Free State. Therefore, chromosomal variation in these three tetraploid specimens confirm the presence of genetic variability in *C. ciliaris* in South Africa.

The highest incidences of meiotic abnormalities were recorded in the pentaploid specimens (Table 2). These abnormalities were mostly the result of an uneven polyploid level. The average number of univalents observed, was approximately half of the average number of chromosome laggards observed (4.0 versus 9.2) (Table 2). There was an increase in the average number of laggards observed (Table 2). This could have been due to amphitelic orientation and equational distribution of the univalents observed during metaphase I, as various chromatid lag-



gards were observed during anaphase I (Figure 3C). These anaphase I laggards were mostly included in more than one micronucleus per cell (Figure 4B, C), as an average frequency of 4.1 micronuclei per cell has been observed.

The average number of laggards observed for this polyploid level, was representative of a complete genome lagging during anaphase I. It is suggested that the genomic constitution of the pentaploid specimens includes one unrelated genome. This suggestion is based on the average number of univalents present, the absence of trivalents and the high average number of laggards observed during anaphase I. A genomic constitution of, for example AAA'A'A", is proposed for this polyploid level. Segmental allopolyploidy is justified by the high and the low occurrence of bivalents and quadrivalents respectively, observed during prophase and metaphase I. Chromosomal variation is evident in this polyploid level, for meiotic chromosome behaviour varied among the specimens studied (Table 2).

The average number of univalents present, the chromosome and chromatid laggards and the micronuclei observed for the hexaploid specimens (2.8, 3.3 and 3.8 respectively), were relatively low when compared to that of the pentaploid specimens (Table 2). A genomic constitution of, for example AAA'A'A"A", is proposed for the hexaploids. Segmental allopolyploidy, based on the abundant bivalent and occasional quadrivalent chromosome configurations found (Figure 2D), is proposed. The presence of quadrivalents indicates a degree of homology between the A and A' genomes.

The genomic constitutions of the various polyploid levels ( $n = 17$ —segmental allopolyploidy;  $n = 18$ —segmental polyploidy to allopolyploidy;  $n = 45/2$ —allopolyploidy and  $n = 27$ —segmental allopolyploidy) indicate the presence of hybridisation in this species.

Hybridisation among plant individuals is usually characterised by various changes in chromosome structure (Darlington 1937; Dobzhansky 1941). For *C. ciliaris*, these changes include the presence of paracentric inversions. These inversions were mostly observed in the tetraploid specimens (Figure 5A–C). The higher occurrence of these inversions could be due to the high number of tetraploid specimens which were cytogenetically studied. The highest average number of cells containing anaphase I bridges was observed in *Spies 5652* (71.4%) (Figure 5A) (Table 2). Different paracentric inversions were found among the specimens, as the chromosome fragments differed in size.

Occasional or recurrent hybridisation and the complete local breakdown of reproductive isolation between sympatric species result in the production of hybrid swarms. These swarms include the whole range of genetic variability of the parental species. This scenario could be representative of *C. ciliaris*, for a wide range of chromosomal, morphological and genetic variation is evident in this species.

## CONCLUSIONS

With the aid of meiotic analyses, a basic chromosome number of  $x = 9$  has been confirmed for *Cenchrus ciliaris*. Polyploidy is common and varies from tetraploid to hexaploid. Aneuploidy was observed in a single specimen. It is suggested that this specimen is the result of loss aneuploidy from two chromosomes of a single genome.

Various meiotic irregularities were observed for this species. The highest incidences of meiotic abnormalities were observed for the pentaploid specimens. This was attributed to their uneven polyploid and chromosome number.

The chromosome abnormalities observed during meiosis were an indication of genomic relationships. These relationships varied among the specimens and the polyploid levels. Segmental allopolyploidy was suggested for the aneuploid specimen, whereas for the tetraploid specimens, it varied from segmental allopolyploidy to allopolyploidy. A genomic constitution of allopolyploidy and segmental allopolyploidy is suggested for the pentaploid and hexaploid levels respectively. The nature of the genomic relationships indicated the presence of hybridisation. Hybridisation in *C. ciliaris* was confirmed by the chromosomal variation observed among specimens in each of the polyploid levels.

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# Invasive alien woody plants of the southern and southwestern Cape region, South Africa

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**Keywords:** alien invasive plants, Forest Biome, Fynbos Biome, roadside survey, Savanna Biome, southern and southwestern Cape, Succulent Karoo Biome

### ABSTRACT

The frequency and abundance of invasive alien plants were recorded along roadsides and at watercourse crossings in 82.9% (145/175) of the quarter degree squares in the study area (31–35°S, 17–25°E and covering ± 90 000 km<sup>2</sup>). The survey yielded 102 species of which the most prominent (in order of prominence) in roadside and veld (natural and modified) habitats were: *Acacia cyclops*, *A. saligna* and *A. mearnsii*. The most prominent species (in order of prominence) in stream-bank habitats were: *A. mearnsii*, *A. saligna* and *Populus × canescens*.

The greatest intensity of invasion was recorded in forest and fynbos vegetation types in the relatively narrow belt stretching from the coastline to the tops of the coastal mountain ranges. In the coastal lowlands *Acacia cyclops* and *A. saligna* form the most extensive and continuous stands of alien vegetation recorded anywhere in South Africa. In the arid interior invasion was largely confined to watercourses.

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### INTRODUCTION

#### Survey history and objectives

This study of the southern and southwestern Cape is the sixth of eight regional surveys which together are designed to reflect invasion by woody alien plants in South Africa as a whole. Surveys have been completed for the former Transvaal (Henderson & Musil 1984), Natal and northeastern Orange Free State (Henderson 1989), Orange Free State (Henderson 1991a), northern Cape (Henderson 1991b) and eastern Cape (Henderson 1992). The survey of this area was undertaken from east to west and during the months of March and October 1990, January and December 1991, February and November 1992, and May 1993.

The objectives of the survey were: to produce a checklist of the major invasive alien woody plants of stream-bank, roadside and veld habitats in the study area; to determine the pattern of alien woody invasion as a whole and for individual species; to attempt to relate distribution to environmental factors and to determine which are the most prominent and potentially important invaders.

#### The study area

The study area lies between latitudes 31° and 35°S and longitudes 17° and 25°E (Figure 1), and occupies an area of approximately 90 000 km<sup>2</sup>. It is bounded in the south by the Indian Ocean and in the southwest by the Atlantic Ocean. The topography is dominated by the mountains of the Cape Fold Belt. These mountains occur for the most part in subparallel ranges with an average height of 1 000 to 1 500 m and with individual peaks reaching over 2 000 m. In the south these ranges strike from east to west whereas in the west the strike is more

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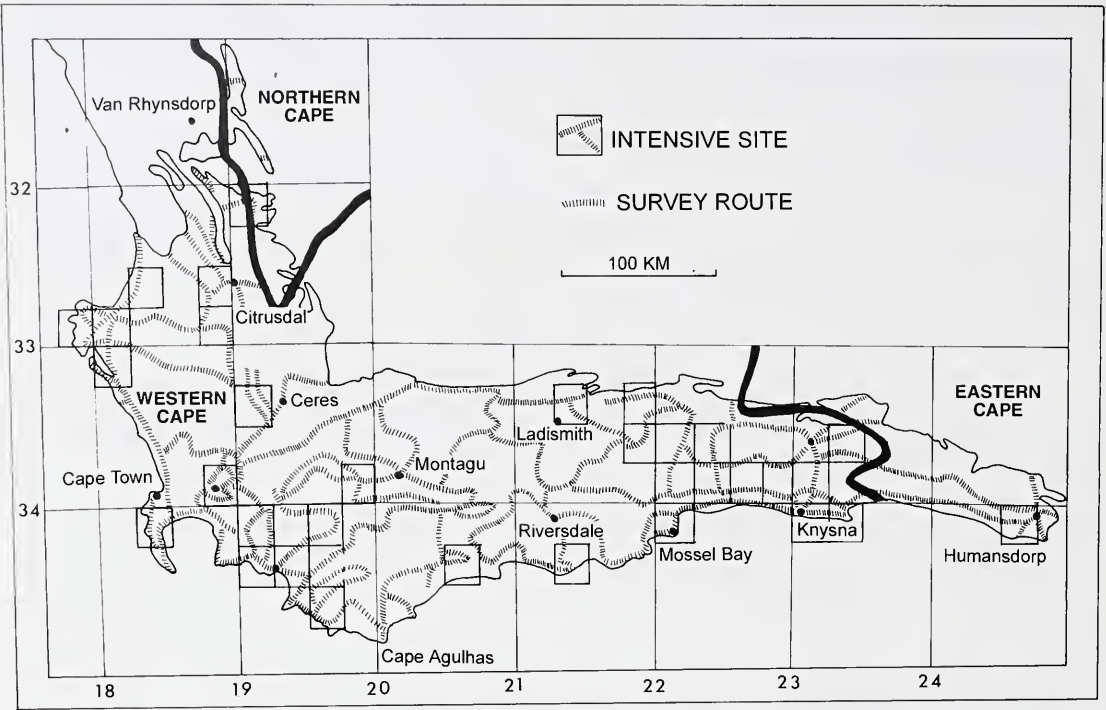


FIGURE 1.—The study area showing survey routes and intensive sites.

nearly north-north-west (Taylor 1978). The ranges are separated by wide intermontane valleys. There are many river systems in the study area which contains about 17% of the major mountain catchments of South Africa, Lesotho and Swaziland (Van der Zel 1981).

Rainfall ranges from 200 mm in the arid interior to 3 600 mm per annum on some of the higher mountains. To the west of 20°E a Mediterranean-type climate prevails with cool wet winters and warm dry summers. In the east, rainfall is more consistent through the year.

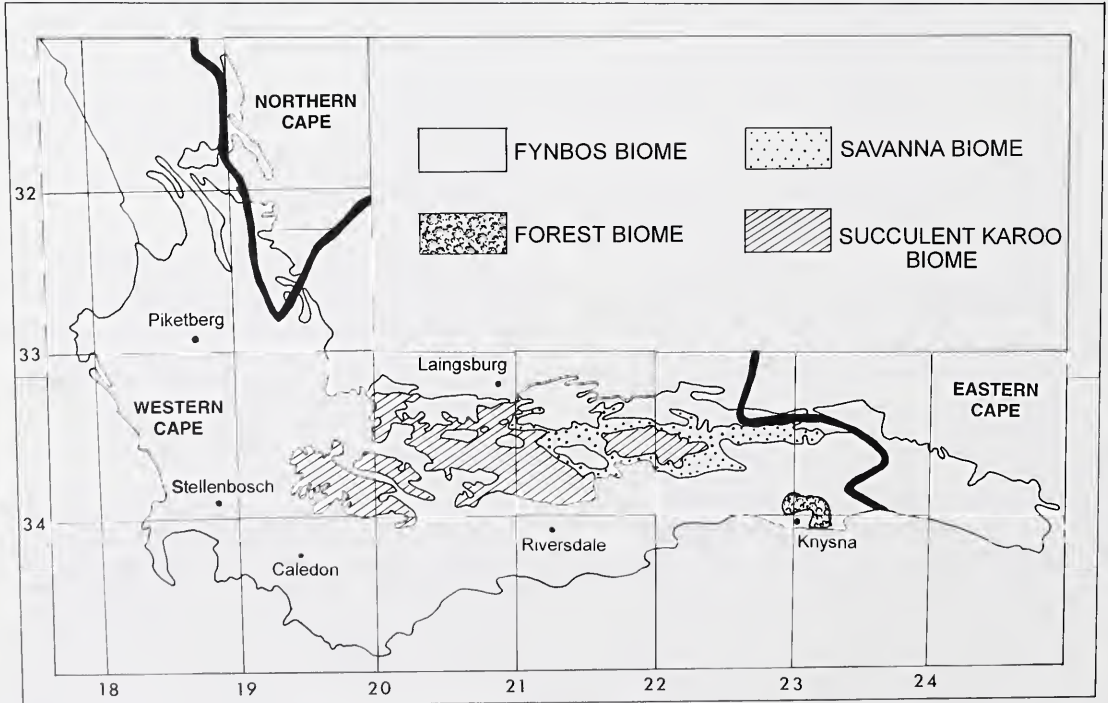


FIGURE 2.—The biomes in the study area after Rutherford & Westfall (1986).



TABLE 1.—Veld type categories in study area and equivalent Acocks Veld Type groupings and Veld Type numbers

Biome* and veld type category*	Acocks Veld Type grouping	Acocks Veld Type No.
<b>Succulent Karoo Biome</b>	IV. Karoo and Karroid Types	26, 31
	IVA. False Karoo Types	43
<b>Savanna Biome</b>	IV. Karoo and Karroid Types	25
<b>Forest Biome</b>	I. Coastal Tropical Forest Types	4
<b>Fynbos Biome</b>		
Strandveld*	IV. Karoo and Karroid Types	34
Mountain renosterveld*	IVA. False Karoo Types	43
Coastal renosterveld*	IV. Karoo and Karroid Types	23
	V. Temperate and Transitional Forest and Scrub Types	46
Coastal fynbos*	V. Temperate and Transitional Forest and Scrub Types	47
Mountain fynbos*	VII. Sclerophyllous Bush Types	69
	VIII. False Sclerophyllous Bush Types	70
Mountain fynbos and forest*	I. Coastal Tropical Forest Types	4

\* according to Henderson; † according to Rutherford & Westfall 1986.

Changes in the rainfall can be very abrupt, and are usually associated with the topography. During winter, snow falls regularly on the higher mountains, but the lowlands enjoy an equable climate and frost is rare except in some of the deep valleys of the interior (Taylor 1978; Linder 1991; Jury 1993).

For the purposes of this survey and in keeping with previous surveys, the vegetation of the study area has been subdivided according to the biomes of southern Africa defined by Rutherford & Westfall (1986) and Acocks's *Veld types of South Africa* (1988). There are four biomes in the study area, namely the Succulent Karoo, Savanna, Forest and Fynbos Biomes (Figure 2). Eleven Acocks Veld Types occur in the study area and have been grouped into nine broad veld type categories for the purposes of this survey (Table 1; Figure 2).

Succulent karoo occupies the region commonly known as the Little Karoo. The vegetation has a predominance of succulents, and dwarf trees and shrubs are numerous. It occupies rocky, hilly country, at elevations ranging from 300–600 m, receiving 150–300 mm of rain per annum (Acocks 1988).

Savanna is represented by a vegetation type commonly known as succulent mountain scrub which occurs on steep mountain slopes. It is typically a dense scrub dominated by *Portulacaria afra*. The altitude ranges from 400–1 060 m, and rainfall ranges from 250–300 mm per annum (Acocks 1988; Low & Rebelo 1996).

The only forest area of biome dimension in South Africa occurs in the southern Cape at Knysna (Rutherford & Westfall 1986). Before the southern Cape forests were heavily exploited and reduced to their present remnant areas, they covered most of the southern Cape coastal region between Mossel Bay and Humansdorp (Von Breitenbach 1972). Today the Knysna Forest and many smaller forest patches occur in a narrow, irregular belt along the southern coastal shelf and foothills of the Outeniqua and Tsitsikamma Mountains (Von Breitenbach 1972). Forest growth is favoured by mild temperatures and a high, well-distributed rainfall (Von Breitenbach 1972). The mean annual rainfall is

800–1 000 mm (Schulze & McGee 1978), but ranges from 500–1 200 mm (Geldenhuys 1993). Altitude ranges from sea level to 1 220 m at the tops of the mountains only 10–37 km inland (Geldenhuys 1993). Small forest outliers occur in fire-free habitats westwards towards the Cape Peninsula (Taylor 1978).

Strandveld is a low-growing, semisucculent and shrubby vegetation type confined to the sandy coastal plains of the west coast. It is transitional between coastal fynbos and succulent karoo. It receives 50–300 mm of rain per annum, mainly in winter (Acocks 1988).

Mountain renosterveld is a karroid-like veld type dominated by renosterbos, *Elytropappus rhinocerotis* (Acocks 1988). It is usually situated between succulent karoo and mountain fynbos and receives 250–400 mm of rain per annum (Low & Rebelo 1996).

Coastal renosterveld occurs in a western and southern belt and is situated between the fynbos of the mountains and of the coastal plain. The terrain is undulating and the soils are clayey. Rainfall ranges from 300–600 mm per annum. Most of the original vegetation has been ploughed up for the growing of wheat. Scrub relics that remain are dense, thorny and semisucculent. Elsewhere the scrub has been replaced mainly by renosterbos (Acocks 1988).

Coastal fynbos occurs on sand and limestone in the west and south coastal belts. The vegetation is a more or less open scrub lacking the dense thorniness and semi-succulence of the previous veld type. The altitude ranges from 0–300 m and rainfall from 300–500 mm per annum (Acocks 1988).

Mountain fynbos is the most widespread vegetation type in the Fynbos Biome, occurring mainly along the Cape Fold Belt from north of Nieuwoudtville to Cape Town and Cape Agulhas and to Humansdorp in the east. Altitude ranges from 0–2 200 m, and rainfall from 200 to more than 2 000 mm per annum, occurring mainly in the winter months (Low & Rebelo 1996). Summers are hot and dry and conducive to veld fires. The vegetation is an open to closed shrubland.

Mountain fynbos & forest occurs outside the Forest Biome defined by Rutherford and Westfall (1986) but within the original limits of the Knysna Forest, Acocks Veld Type 4, mapped by Acocks (1988). This region contains wet mountain fynbos (National Committee for Remote Sensing, CSIR 1983), numerous small patches of forest, including the Tsitsikamma Forest, and extensive timber plantations of mainly pine, but also gums and *Acacia melanoxylon* (Van der Zel 1988). The mean annual rainfall is 800–1 000 mm (Schulze & McGee 1978) and uniformly distributed throughout the year.

## METHOD

### Sampling method

The method used in this survey was the same as in the previous survey of the eastern Cape (Henderson 1992). The presence and abundance of all alien trees, large shrubs and conspicuous climbers which appeared to be spreading spontaneously (naturalised) were recorded for each veld type category, habitat type (roadsides and adjoining veld, and streambanks) and quarter degree/fifteen minute square traversed by road. Thirty three quarter degree squares were selected for more intensive surveying (Figure 1). They may be used at a later date for a quick resurvey of the study area to assess any changes that may have taken place.

Recordings of roadside and veld invaders were made from a moving vehicle along road transects of between five and 10 km in length. The average transect length was 6.4 km for the general survey area and 5.0 km for the intensive sites. Recordings of streambank invaders were made at virtually all watercourse crossings on the survey route. Details of the roads traversed are lodged in the Plant Protection Research Institute (PPRI), Pretoria. As on the previous occasions the survey was undertaken in a minibus, with one driver and one recorder (the author). The average speed was 60 km/h but ranged from about 20 km/h in densely vegetated areas to 100 km/h in sparsely vegetated areas.

All the raw data for this survey as well as the previously completed regional surveys have been computerized using the data management system DataEase. This database is housed in Pretoria at the PPRI.

### Abundance ratings

The abundance ratings for roadside and veld habitats and streambank habitats are given in Table 2.

### Sampling level achieved

The sampling level achieved was 82.9% (145 out of the total 175 quarter degree squares) at an average of 44.5 km travelled per square. An average of 29.3 km of road transects were sampled per quarter degree square for abundance estimates of roadside and veld invaders.

The veld type coverage in terms of quarter degree squares and road transects sampled, kilometres travelled and watercourse recordings made, is given in Table 3. Statistics for streambank, roadside and veld habitats are given in Tables 4 and 5.

### Data treatment—formulae used

#### Frequency

The percentage frequency of occurrence of a species *x* in a given category (veld type, biome or study area) *y* was calculated as follows:

$$\text{frequency} = \frac{\text{no. of watercourse recordings/road transects in category } y \text{ having species } x}{\text{total no. of watercourse recordings/road transects in category } y} \times 100$$

#### Prominence value

The prominence value is a combined measure of a species' frequency and abundance relative to that of all

TABLE 2.—Abundance ratings

Rating	Roadsides and veld	No. *	Streambanks	Rating
9	A virtually continuous, almost pure stand	1000+	Any number, with cover more than 75% of the reference area	7
8	The commonest species in a generally continuous tree or shrub layer	500–999	Any number, with 50–75% cover	6
7	Less abundant than above but greater than 20 individuals or groups per km	200–499	Any number, with 25–50% cover	5
6	10–20 individuals or groups per km	100–199	Any number, with 5–25% cover	4
5	5–10 individuals or groups per km	50–99	Numerous, but less than 5% cover or scattered, with cover up to 5%	3
4	2–5 individuals or groups per km	20–49	Few, with small cover	2
3	± 1 individual or group per km	5–19	Solitary, with small cover	1
2	Less abundant than above but more than 1 individual or group per 5 km	2–4		
1	± 1 plant or group per 5–10 km	1		

\* approximate numbers of individuals or groups per 10 km transect.

other species, within a given vegetation category (veld type, biome or study area).

In streambank habitats the prominence value for a species *x* in category *y* was calculated as follows:

$$\text{prominence value} = \frac{\frac{\text{total weighted abundance of species } x \text{ in category } y}{\text{sum of the weighted abundances of all species in category } y} \times 100}{\frac{\text{frequency of species } x \text{ in category } y}{\text{sum frequency of all species in category } y} \times 100}$$

The abundance ratings were weighted according to the minimum percentage cover in each scale rating (see Table 2). Thus ratings 7, 6, 5 and 4 had weighted values of 75, 50, 25 and 5 respectively. Ratings 1, 2 and 3 each had weighted values of 1.

In roadside and veld habitats the prominence value for a species *x* in category *y* was calculated as follows:

$$\text{prominence value} = \frac{\frac{\text{total abundance* of species } x \text{ in category } y}{\text{sum of the abundances* of all species in category } y} \times 100}{\frac{\text{frequency of species } x \text{ in category } y}{\text{sum frequencies of all species in category } y} \times 100}$$

The highest prominence values in a given category which add up to approximately 160 points out of a total of 200 are printed in bold in Tables 6, 7, 8 and 9. The cut-off point of 160 points is arbitrary but represents 80% of the summed prominence values.

*Mean species abundance rating in roadside and veld habitats* (Tables 8 & 9)

The mean species abundance rating\*\* of a species *x* in a given category (veld type, biome or study area) *y* was calculated as follows:

$$\text{mean no. of individuals or groups per 10 km} = \frac{\text{total no. of individuals or groups of species } x \text{ in category } y}{\text{total distance along which species } x \text{ was rated in category } y} \times 10$$

*Mean abundance of invaders per km in roadside and veld habitats* (Table 5)

The mean abundance of invaders per km in a given category (veld type, biome or study area) *y*/quarter degree square *z* was calculated as follows:

$$\text{mean abundance} = \frac{\frac{\text{total abundance* of all species in category } y/\text{quarter degree square } z}{\text{total kilometres rated for abundance estimates in category } y/\text{quarter degree square } z}}$$

\* each abundance rating was expressed in numbers of individuals or groups recorded per transect (Table 2). To be both conservative and consistent the minimum number was used in each instance, e.g. an abundance rating of 5 over 10 km = 50 and an abundance rating of 5 over 5 km = 25.

\*\* mean no. of individuals or groups per 10 km converted to rating (Table 2).

## RESULTS

The survey yielded 102 naturalised alien species. These species are listed in the Appendix together with a further 34 species which were obtained from various literature and other sources. The distributions of 20 of the most prominent species are given in Figures 6 and 7 and a further 10 potentially important species are given in Figure 8.

### The streambank habitat

#### *The whole study area*

One thousand and thirty-six watercourse crossings were sampled in which 75 species were recorded, with up to eight species in one sample. Invaders were present at 73.5% of all crossings and 30.9% of all crossings were heavily invaded (Table 4).

#### *Analysis according to veld type*

Overall the Fynbos Biome was the most heavily invaded in terms of percentage crossings invaded and percentage crossings heavily invaded. Invasion was most intense in mountain and coastal fynbos where the highest percentages of heavily invaded crossings were recorded. Very few watercourses were sampled in the Forest Biome. Most recordings were of small streams and it was difficult to see beyond 10 m.

#### *Analysis according to species*

##### Frequency

*Acacia mearnsii* was the most frequently recorded invader in the study area (29.4%). Only this species, *A. saligna* (20.7%) and *Populus × canescens* (13.6%) were recorded at 10% or more crossings in the whole study area (Table 7).

In the Fynbos Biome the most frequently recorded species were *Acacia mearnsii* (40.4%), *A. saligna* (30.7%), *Populus × canescens* (17.1%) and *A. cyclops* (11.2%). In the Forest Biome *A. melanoxylon* (70.6%), *A. mearnsii* (35.3%) and *Eucalyptus diversicolor* (23.5%) were the most frequent invaders. In the Savanna Biome *Nicotiana glauca* (14.1%), *Arundo donax* (11.1%), *Populus × canescens* (11.1%) and *Ricinus communis* (11.1%) were the most frequently recorded species. In the Succulent Karoo Biome *Acacia saligna* (15.6%) and *Nicotiana glauca* (15.6%) were the most frequent invaders.

##### Prominence

The most prominent invader in the whole study area was *Acacia mearnsii* with a prominence value of 61.6 out of a combined total for all species of 200 (Table 7). The next most prominent invaders were *A. saligna* (36.9) and *Populus × canescens* (19.5).

In the Fynbos Biome *Acacia mearnsii* was the most prominent invader in four of the six veld type categories, namely mountain fynbos, mountain fynbos & forest,



TABLE 3.—Sampling coverage of each biome, veld type category and study area

Biome <sup>†</sup> and veld type category <sup>†</sup>	1/4 degree squares	Road transects	Distance (km)*	Watercourse recordings
Succulent Karoo Biome	29	77	569	224
Savanna Biome	14	36	219	99
Forest Biome	4	27	132	17
Fynbos Biome	133	520	3332	696
Strandveld <sup>†</sup>	14	38	190	7
Mountain renosterveld <sup>†</sup>	32	57	418	89
Coastal renosterveld <sup>†</sup>	52	133	921	250
Coastal fynbos <sup>†</sup>	30	72	499	71
Mountain fynbos <sup>†</sup>	64	169	1042	214
Mountain fynbos & forest <sup>†</sup>	15	51	262	65
Study area	145	660	4252	1036

\* this represents the distance along which abundance recordings were made. Total distance along which observations were made is approximately one and a half times that given; <sup>†</sup> according to Henderson; <sup>‡</sup> according to Rutherford & Westfall 1986.

TABLE 4.—Statistics for streambanks in each biome, veld type category and study area

Biome <sup>†</sup> and veld type category <sup>†</sup>	Total no. of spp.	Average no. of spp./crossing	Max. no. of spp./crossing	% crossings heavily invaded*	% crossings invaded**
Succulent Karoo Biome	26	1.0	6	11.6	51.8
Savanna Biome	22	0.9	6	2.0	45.5
Forest Biome	8	1.5	4	17.6	76.5
Fynbos Biome	70	1.8	8	41.5	84.3
Strandveld <sup>†</sup>	7	1.3	4	28.6	71.4
Mountain renosterveld <sup>†</sup>	23	0.9	5	19.1	55.1
Coastal renosterveld <sup>†</sup>	50	1.9	8	39.0	83.2
Coastal fynbos <sup>†</sup>	22	2.0	6	50.7	94.4
Mountain fynbos <sup>†</sup>	52	1.9	6	54.7	91.6
Mountain fynbos & forest <sup>†</sup>	21	2.0	6	30.8	95.4
Study area	75	1.5	8	30.9	73.5

\* one or more species scored an abundance rating of 5 or more; \*\* invaders present; <sup>†</sup> according to Henderson; <sup>‡</sup> according to Rutherford & Westfall 1986.

TABLE 5.—Statistics for roadside and veld habitats in each biome, veld type category and study area

Biome <sup>†</sup> and veld type category <sup>†</sup>	Total no. of spp.	Average no. of spp./1/4° sq.	Max. no. of spp./1/4° sq.	% transects invaded	% transects heavily invaded*	Mean abundance of invaders per km**
Succulent Karoo Biome	28	5.6	14	93.5	3.9	1.4
Savanna Biome	18	4.8	9	86.1	0.0	0.9
Forest Biome	31	14.3	28	96.3	88.9	25.1
Fynbos Biome	92	8.5	45	94.2	52.9	14.2
Strandveld <sup>†</sup>	12	3.4	7	94.7	28.9	5.9
Mountain renosterveld <sup>†</sup>	35	3.9	11	84.2	7.0	1.8
Coastal renosterveld <sup>†</sup>	71	9.3	45	96.2	46.6	9.5
Coastal fynbos <sup>†</sup>	41	6.6	18	100.0	75.0	29.8
Mountain fynbos <sup>†</sup>	70	10.8	38	91.7	56.2	14.2
Mountain fynbos & forest <sup>†</sup>	49	14.9	29	100.0	96.1	27.4
Study area	96	8.1	45	93.8	45.8	12.2

\* one or more species scored an abundance rating of 5 or more; \*\* see data treatment—formulae used; <sup>†</sup> according to Henderson; <sup>‡</sup> according to Rutherford & Westfall 1986.

TABLE 6.—Alien species occurring in streambank habitats of Succulent Karoo, Savanna and Forest Biomes and in strandveld and mountain renosterveld of Fynbos Biome

Biome and veld type category	Succulent Karoo Biome			Savanna Biome			Forest Biome			Fynbos Biome Strandveld			Mountain renosterveld		
	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P
No. watercourse crossings	224			99			17			7			89		
<i>Acacia cyclops</i>	2.7		3.2							14.3		12.0	6.7	2.2	11.0
<i>dealbata</i>													3.4		5.0
<i>mearnsii</i>	7.6	2.7	<b>25.3</b>	1.0		1.6	35.3	5.9	<b>51.8</b>				23.6	9.0	<b>81.1</b>
<i>melanoxylon</i>	*			*			70.6	17.6	<b>116.9</b>	14.3		12.0			
<i>saligna</i>	15.6	4.0	<b>53.1</b>							42.9	14.3	<b>80.2</b>	7.9	1.1	<b>15.7</b>
<i>Agave americana</i>	1.8		2.1										2.2		2.6
<i>Ailanthus altissima</i>	*			1.0		1.6									
<i>Arundo donax</i>	9.4	1.8	<b>19.1</b>	11.1		<b>19.4</b>							1.1		1.3
<i>Atriplex nummularia</i>	2.7		3.2	2.0		5.0							*		
<i>Casuarina</i> sp.	0.4		0.5												
<i>Eucalyptus</i>															
cf. <i>camaldulensis</i>	8.0	2.7	<b>21.5</b>	3.0		<b>8.4</b>							1.1		1.3
<i>cladocalyx</i>	*			1.0		1.6									
<i>diversicolor</i>							23.5		17.9						
<i>exserta</i>										28.6	14.3	<b>71.8</b>			
<i>leucoxylon</i>	*														
spp.	1.3		1.6	3.0		4.8							*		
<i>Ficus carica</i>	0.4		0.5	3.0		4.8									
<i>Melia azedarach</i>	0.9		1.1	1.0		1.6									
<i>Morus alba</i>				1.0		1.6									
<i>Nerium oleander</i>	0.4		0.5	4.0		6.3							1.1		1.3
<i>Nicotiana glauca</i>	15.6		<b>18.6</b>	14.1		<b>22.3</b>				*			2.2		2.6
<i>Opuntia ficus-indica</i>	0.4		0.5										1.1		1.3
<i>Phoenix canariensis</i>	0.4		0.5												
<i>Pinus</i>															
<i>pinaster</i>							5.9		4.5				1.1		1.3
<i>radiata</i>							*								
<i>Populus</i>															
× <i>canescens</i>	4.9	0.9	<b>10.6</b>	11.1	2.0	<b>66.2</b>				14.3		12.0	16.9	6.7	<b>45.5</b>
<i>deltoides</i>				1.0		1.6							1.1		1.3
<i>nigra</i> 'italica'				*									1.1		1.3
<i>Prosopis</i> spp.	1.8		2.1							14.3		12.0			
<i>Prunus persica</i>				1.0		1.6							1.1		1.3
<i>Pyrus</i> sp.													*		
<i>Quercus robur</i>				1.0		1.6	5.9		4.5				1.1		1.3
<i>Ricinus communis</i>	7.6		9.0	11.1		<b>17.6</b>							*		
<i>Robinia pseudoacacia</i>															
<i>Rubus fruticosus</i>							5.9		4.5						
<i>Salix babylonica</i>	2.2	0.4	5.1	8.1		<b>14.6</b>	*						11.2	1.1	<b>16.5</b>
<i>Schinus molle</i>	3.1		3.7	8.1		<b>12.8</b>							5.6		6.7
<i>Sesbania punicea</i>	7.1	0.4	<b>12.6</b>												
<i>Tamarix</i> spp.	4.5		5.7	2.0		5.0							1.1		1.3

F, % frequency of occurrence; I, % crossings heavily invaded; P, prominence value; \* species occurring in the given category but not included in a formal recording at a watercourse crossing. Bold numbers: the highest prominence values in a given category which add up to ± 80% of the summed values (see text).

coastal renosterveld and mountain renosterveld. *A. saligna* was the most prominent invader in the remaining two categories, namely strandveld and coastal fynbos. *A. cyclops* was a close second in coastal fynbos.

*Acacia melanoxylon* was the most prominent invader in the Forest Biome, followed by *Acacia mearnsii*. *Populus* × *canescens* was the most prominent invader in the Savanna Biome and *A. saligna* was the most prominent invader in the Succulent Karoo Biome.

Roadside and veld habitats

The whole study area

One hundred and forty-five quarter degree squares and 660 road transects were sampled in which 96 species

were recorded. Up to 45 species were recorded per quarter degree square. Naturalised species were recorded in 93.8% of all transects sampled and 45.8% of all transects were heavily invaded (Table 5).

Analysis according to veld type

The most intense invasion was recorded in mountain fynbos & forest in the Fynbos Biome, closely followed by the Forest Biome where the highest percentages of transects (96.1% and 88.9% respectively) were heavily invaded. The mean abundance of invaders per km reached a maximum in coastal fynbos (29.8). The least invasion was recorded in the Savanna Biome, where no transects were heavily invaded.

It must be noted here that although invasion was intense in the Forest Biome, most invasion was recorded in the dis-

TABLE 7.—Alien species occurring in streambank habitats in coastal renosterveld, coastal fynbos, mountain fynbos, mountain fynbos & forest of Fynbos Biome and study area

Biome and veld type category	Coastal renosterveld			Coastal fynbos			Fynbos Biome Mountain fynbos			Mountain fynbos & forest			Total			Total study area		
No. watercourse crossings	250			71			214			65			696			1036		
	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P
<i>Acacia</i>																		
<i>baileyana</i>	*						0.5		0.3	6.2		3.4	0.1		0.1	0.1		0.1
<i>cyclops</i>	11.2	1.2	8.7	54.9	16.9	53.4	12.6	1.9	8.3				11.2	2.4	11.3	8.1	1.6	10.0
<i>dealbata</i>	1.2	0.8	1.5				7.0	6.1	12.1				3.0	2.2	5.4	2.0	1.4	4.7
<i>elata</i>							*						*			*		
<i>longifolia</i>	6.4	3.6	9.9	15.5	5.6	15.6	11.7	5.6	11.9	1.5		1.2	7.6	3.6	9.8	5.1	2.4	8.5
<i>nearnsii</i>	36.4	21.2	63.5	5.6	2.8	9.0	51.4	32.2	76.7	84.6	27.7	118.6	40.4	21.6	67.1	29.4	15.2	61.6
<i>melanoxylon</i>	3.2	0.4	2.8	1.4		0.8	3.3	0.5	2.5	38.5	6.2	31.1	6.0	0.9	4.9	5.2	0.9	5.7
<i>podalyriifolia</i>	*						0.5		0.3				0.1		0.1	0.1		0.1
<i>pycnantha</i>							1.9		1.2				0.6		0.4	0.4		0.3
<i>saligna</i>	34.0	11.6	46.6	46.5	25.3	73.2	23.8	10.3	27.3	*			30.7	11.5	39.8	20.7	7.7	36.9
<i>Agave americana</i>	0.4		0.2				0.5		0.3				0.6		0.4	0.8		0.6
<i>Ailanthus altissima</i>																0.1		0.1
<i>Arundo donax</i>	6.4	0.4	4.3	8.5	1.4	5.9	4.2		2.4	1.5		0.8	4.7	0.3	3.2	6.3	0.6	5.5
<i>Atriplex nummularia</i>																0.8		0.6
<i>Bambusa balcooa</i>				2.8		1.5	*						0.3		0.2	0.2		0.1
<i>Bambuseae</i> sp.										1.5		0.8	0.1		0.1	0.1		0.1
<i>Canna</i> sp.		*											*			*		
<i>Casuarina</i> sp.																0.1		0.1
<i>Colocasia</i> cf. <i>esculenta</i>	*						0.5		0.3				0.1		0.1	0.1		0.1
<i>Cortaderia selloana</i>							0.5		0.3	1.5		0.8	0.3		0.2	0.2		0.1
<i>Eucalyptus</i>																		
cf. <i>camaldulensis</i>	4.0	0.8	3.6	1.4		0.8	4.2	1.4	3.5				3.0	0.7	2.7	4.1	1.1	4.7
<i>cladocalyx</i>	2.4		1.4	*			2.3		1.3				1.6		1.0	1.2		0.9
<i>diversicolor</i>	0.8		0.5	*			1.4		0.8	15.4	1.5	10.4	2.2	0.1	1.4	1.8	0.1	1.4
<i>exserta</i>													0.3	0.1	0.5	0.2	0.1	0.4
<i>globulus</i>							0.5		0.3				0.1		0.1	0.1		0.1
<i>gomphocephala</i>							*						*			*		
<i>lehmannii</i>	1.6		0.9	4.2		2.5	0.5		0.3				1.1		0.7	0.8		0.6
<i>leucosylon</i>																*		
<i>regnans</i>	0.4		0.2				*						0.1		0.1	0.1		0.1
spp.	1.6		0.9				1.4		0.8				1.0		0.6	1.3		0.9
<i>Ficus carica</i>	0.4		0.2	1.4		0.8	*						0.3		0.2	0.6		0.4
<i>Hakea sericea</i>							0.5		0.3	3.1		1.7	0.4		0.2	0.3		0.2
<i>Ipomoea</i>																		
<i>nil</i>	*												*			*		
cf. <i>purpurea</i>	0.4		0.2										0.1		0.1	0.1		0.1
<i>Lantana camara</i>	0.4		0.2				0.9		0.5				0.4		0.2	0.3		0.2
<i>Melia azedarach</i>	0.8		0.5										0.3		0.2	0.5		0.4
<i>Morus alba</i>																0.1		0.1
<i>Myoporum tenuifolium</i>							*						*			*		
<i>Nerium oleander</i>	0.4		0.2										0.3		0.2	0.7		0.5
<i>Nicotiana glauca</i>	4.4		2.5	4.2		2.3	0.5		0.3				2.4		1.4	6.4		4.6
<i>Opuntia</i>																		
<i>ficus-indica</i>	4.8		2.8	1.4		0.8	0.5		0.3				2.2		1.3	1.5		1.1
<i>vulgaris</i>				1.4		0.8	0.5		0.3				0.3		0.2	0.2		0.1
<i>Paraserianthes lophantha</i>	4.8		3.0	5.6		3.0	6.5	0.5	4.0	4.6		2.9	4.7		0.1	3.2	0.1	2.6
<i>Passiflora caerulea</i>	2.4		1.4										0.9		0.5	0.6		0.4
<i>Phoenix</i>																		
<i>canariensis</i>	*			1.4		0.8							0.1		0.1	0.2		0.1
<i>dactylifera</i>	0.8		0.5										0.3		0.2	0.2		0.1
<i>Phytolacca dioica</i>	2.4		1.4				*						0.9		0.5	0.6		0.4
<i>Pinus</i>																		
<i>halepensis</i>							0.5		0.3				0.1		0.1	0.1		0.1
<i>pinaster</i>	0.8		0.5				2.3		1.3	16.9		9.6	2.7		1.7	1.9		1.4
<i>pinea</i>	*												*			*		
<i>radiata</i>	0.4		0.2				0.9		0.5	6.2		3.4	1.0		0.6	0.7		0.5
<i>Pittosporum undulatum</i>	0.4		0.2										0.1		0.1	0.1		0.1
<i>Populus</i>																		
× <i>canescens</i>	17.6	6.8	18.3	22.5	5.6	18.5	18.7	7.9	21.1	4.6	1.5	6.9	17.1	6.5	19.9	13.6	4.7	19.5
<i>deltoides</i>							0.9		0.5				0.4		0.2	0.4		0.3
<i>nigra</i> 'italica'							0.5		0.3				0.3		0.2	0.2		0.1
<i>Prosopis</i> spp.	4.0		2.3				1.4		0.8				2.0		1.2	1.7		1.2
<i>Prunus persica</i>	2.0		1.1	1.4		0.8	0.9		0.5				1.3		0.8	1.0		0.7
<i>Psidium guajava</i>	0.4		0.2	2.8		1.5	0.5		0.3				0.6		0.4	0.4		0.3
<i>Punica granatum</i>	*												*			*		
<i>Pyrus</i> sp.							0.5		0.3				0.1		0.1	0.1		0.1
<i>Quercus</i>																		
<i>robur</i>	2.8		1.7				3.7		2.0	3.1		1.7	2.4		1.5	1.8		1.3
spp.	0.8		0.5										0.3		0.2	0.2		0.2



TABLE 7 (cont.).—Alien species occurring in streambank habitats in coastal renosterveld, coastal fynbos, mountain fynbos, mountain fynbos & forest of Fynbos Biome and study area

Biome and veld type category	Coastal renosterveld			Coastal fynbos			Fynbos Biome Mountain fynbos			Mountain fynbos and forest			Total			Total study area		
No. watercourse crossings	250			71			214			65			696			1036		
	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P
<i>Ricinus communis</i>	6.8		3.9	7.0		3.8	4.7		2.6	3.1		1.7	5.0		3.0	6.1		4.4
<i>Robinia pseudoacacia</i>													*			*		
<i>Rosa eglanteria</i>							0.9		0.5				0.3		0.2	0.2		0.1
<i>Rubus flagellaris</i>													0.1		0.1	0.1		0.1
<i>Rubus fruticosus</i>	6.4	0.8	<b>4.7</b>				9.3	0.9	<b>6.0</b>	3.1		1.7	5.5	0.6	4.0	3.8	0.4	3.4
<i>Salix babylonica</i>	3.2		1.8	8.5		4.6	3.3	0.5	2.2	1.5		0.8	4.6	0.3	3.1	4.3	0.3	3.6
<i>cf. fragilis</i>							0.5	0.5	0.6				0.1	0.1	0.2	0.1	0.1	0.2
<i>Schinus molle</i>	0.4		0.2				*						0.9		0.5	2.0		1.4
<i>Senna sp.</i>	0.4		0.2										0.1		0.1	0.1		0.1
<i>Sesbania punicea</i>	5.6	0.4	<b>3.9</b>				7.0	0.5	4.3	*			4.2	0.3	2.9	4.3	0.3	3.8
<i>Solanum mauritianum</i>	2.4		1.4				*			3.1		1.7	1.1		0.7	0.8		0.6
<i>Spartium junceum</i>							*						*			*		
<i>Tamarix spp.</i>	0.8		0.5										0.4		0.3	1.4		1.1

F, % frequency of occurrence; I, % crossings heavily invaded; P, prominence value; \* species occurring in the given category but not included in a formal recording at a watercourse crossing. Bold numbers: the highest prominence values in a given category which add up to ± 80% of the summed values (see text).

turbed areas between the remaining indigenous forest patches. Only small sections of forest are accessible by road. The following species were recorded along roadsides, margins or other gaps in indigenous forest: *Acacia mearnsii*, *A. melanoxylon*, *Cinnamomum camphora*, *Cortaderia selleana*, *Eucalyptus diversicolor*, *Pinus pinaster*, *P. radiata*, and *Rubus fruticosus*. They were never abundant but occurred as single plants or small groups.

Most of the higher parts of the mountain fynbos were inaccessible by road and therefore undersampled in this survey. As a consequence the mountain species such as *Hakea* spp., particularly *H. sericea*, and *Pinus* spp. were no doubt under-recorded in this survey. The accessible parts of mountain fynbos were the valleys and this is where most recordings were done. The best data on the extent of woody plant invasions in the higher altitude areas can be obtained from studies of the Cape Peninsula mountains (Moll & Trinder-Smith 1992; Richardson *et al.* 1996).

Analysis according to species

Frequency

The most frequently recorded species in the whole study area were *Opuntia ficus-indica* (71.5%), *Acacia saligna* (67.0%), *A. cyclops* (63.6%), *Nicotiana glauca* (63.6%), *A. mearnsii* (52.9%), *Pinus pinaster* (38.8%) and *A. melanoxylon* (33.5%).

The most frequently recorded species in the Fynbos Biome were *Acacia cyclops*, *A. saligna* and *A. mearnsii*. In the Forest Biome *A. melanoxylon*, *A. mearnsii*, *Pinus pinaster* and *P. radiata* were the most frequent species. In the Savanna Biome *Nicotiana glauca*, *Opuntia ficus-indica* and *Agave americana* were the most frequent species. In the Succulent Karoo Biome *Nicotiana glauca*, *Opuntia ficus-indica* and *A. saligna* were the most frequent species.

Prominence

*Acacia cyclops* scored the highest prominence value of 45.2 in the study area. The next most prominent species were *Acacia saligna* (24.8) and *A. mearnsii* (24.0) (Table 9).

In the Fynbos Biome, the three aforementioned species were the most prominent invaders, followed by *Pinus pinaster*. In the Forest Biome *Acacia melanoxylon* was the most prominent invader followed by *A. mearnsii*, *Pinus pinaster* and *P. radiata*. In the Savanna Biome *Nicotiana glauca* and *Opuntia ficus-indica* were the most prominent species. In the Succulent Karoo Biome *A. saligna* was the most prominent species.

Patterns of invasion

Alien plant invasion was recorded in streambank, roadside and veld habitats throughout the southern and southwestern Cape (Figures 3, 4 & 5). Most invasion, however, was encountered within the relatively narrow belt stretching from the coastline to the tops of the coastal mountain ranges.

A comparison of Figures 3 and 4 shows that similar patterns of invasion were recorded in streambank, roadside and veld habitats except that in the dry inland areas of the Little Karoo, centred around Ladismith and Oudtshoorn, there was more severe invasion of the streambank habitat than of roadside and veld habitats.

DISCUSSION

Prominent and potentially important species

*Acacia* species were overall the most prominent invaders in the study area with one or more species being the most prominent in every vegetation category with the

TABLE 8.—Alien species occurring in roadside and veld habitats of Succulent Karoo, Savanna and Forest Biomes and in strandveld and mountain renosterveld of Fynbos Biome

Biome and veld type category	Succulent Karoo Biome			Savanna Biome			Forest Biome			Fynbos Biome Strandveld			Mountain renosterveld		
	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P
No. road transects	77			36			27			38			57		
<i>Acacia</i>															
<i>baileyana</i>							*						*		
<i>cyclops</i>	18.2	3.0	<b>20.8</b>				25.9	3.0	5.8	89.5	4.0	<b>112.3</b>	17.5	4.0	<b>45.4</b>
<i>elata</i>							7.4	2.0	1.5						
<i>longifolia</i>							7.4	3.0	1.8						
<i>mearnsii</i>	13.0	3.0	<b>11.8</b>				81.5	5.0	<b>37.0</b>				35.1	3.0	<b>33.7</b>
<i>melanoxydon</i>							88.9	6.0	<b>60.8</b>						
<i>pycnantha</i>	*														
<i>saligna</i>	29.9	3.0	<b>38.5</b>				11.1	3.0	2.5	42.1	3.0	<b>25.9</b>	17.5	3.0	<b>15.3</b>
<i>Agave americana</i>	26.0	2.0	<b>15.5</b>	33.3	1.0	<b>23.6</b>							22.8	2.0	<b>13.0</b>
<i>Arundo donax</i>	5.2	1.0	2.5	2.8	1.0	1.8							*		
<i>Atriplex nummularia</i>	10.4	2.0	<b>6.7</b>	2.8	2.0	2.3				7.9	2.0	4.1	1.8	1.0	1.0
<i>Brugmansia</i> × <i>candida</i>							3.7	1.0	0.7				*		
<i>Canna</i> sp.							*								
<i>Cereus jamacaru</i>													1.8	1.0	1.0
<i>Cestrum</i> cf. <i>laevigatum</i>										*					
<i>Cinnamomum camphora</i>							3.7	1.0	0.7						
<i>Cortaderia selloana</i>							7.4	1.0	1.5				*		
<i>Echinopsis spachiana</i>	1.3	1.0	1.1	*									*		
<i>Eucalyptus</i>															
<i>canaldulensis</i>	2.6	1.0	1.3				*						*		
<i>cladocalyx</i>	1.3	1.0	1.1										7.0	1.0	3.5
<i>diversicolor</i>							29.6	4.0	<b>11.1</b>						
<i>globulus</i>							*								
<i>gomplocephala</i>										2.6	2.0	1.4			
spp.	5.2	1.0	2.7	2.8	1.0	1.8	48.1	3.0	<b>11.5</b>				10.5	2.0	<b>6.7</b>
<i>Ficus carica</i>	3.9	2.0	2.0	5.6	1.0	3.6							3.5	1.0	1.8
<i>Fraxinus angustifolia</i>	1.3	1.0	1.1	2.8	1.0	1.8									
<i>Gleditsia triacanthos</i>													1.8	2.0	1.0
<i>Grevillea robusta</i>							3.7	1.0	0.7						
<i>Hakea sericea</i>							7.4	3.0	1.8				3.5	2.0	1.9
<i>Ipomoea</i> cf. <i>purpurea</i>							3.7	1.0	0.7						
<i>Lavatera arborea</i>										10.5	4.0	10.1			
<i>Lepospermum laevigatum</i>							3.7	1.0	0.7						
<i>Melia azedarach</i>	2.6	2.0	1.4										*		
<i>Myoporium tenuifolium</i>							*			13.2	2.0	6.6			
<i>Nerium oleander</i>				2.8	1.0	1.8									
<i>Nicotiana glauca</i>	42.9	2.0	<b>31.6</b>	61.1	3.0	<b>67.1</b>				29.0	4.0	<b>28.7</b>	7.0	3.0	5.9
<i>Opuntia</i>															
<i>ficus-indica</i>	37.7	2.0	<b>28.7</b>	55.6	2.0	<b>59.5</b>				*			49.1	3.0	<b>38.6</b>
<i>imbricata</i>	2.6	1.0	1.3	2.8	1.0	1.8							1.8	1.0	1.0
<i>microdasys</i>				*											
<i>robusta</i> cvs	7.8	2.0	4.3	5.6	1.0	4.1							1.8	2.0	1.0
<i>vulgaris</i>	2.6	1.0	1.3												
<i>Paraserianthes lophantha</i>							*			*			*		
<i>Phytolacca dioica</i>							3.7	1.0	0.7						
<i>Pinus</i>															
<i>halepensis</i>				*									8.8	2.0	<b>6.0</b>
<i>pinaster</i>							74.1	5.0	<b>29.5</b>				1.8	2.0	1.0
<i>radiata</i>							70.4	4.0	<b>20.7</b>				3.5	1.0	1.8
sp.													1.8	1.0	1.0
<i>Populus</i> × <i>canescens</i>	*			2.8	1.0	1.8	*						3.5	2.0	1.9
<i>Prosopis</i> spp.	2.6	1.0	1.3							13.2	2.0	6.7	1.8	1.0	1.0
<i>Prunus</i>															
<i>armeniaca</i>	2.6	2.0	1.4										5.3	2.0	2.8
<i>persica</i>	3.9	1.0	1.9				3.7	1.0	0.7				10.5	1.0	5.5
<i>Pyracantha angustifolia</i>							3.7	1.0	0.7						
<i>Pyrus</i> sp.													3.5	2.0	2.0
<i>Quercus robur</i>							3.7	1.0	0.7						
<i>Ricinus communis</i>	13.0	3.0	<b>10.1</b>	16.7	2.0	<b>15.4</b>	3.7	1.0	0.7	10.5	2.0	5.5			
<i>Robinia pseudoacacia</i>							3.7	1.0	0.7						
<i>Rubus fruticosus</i>	2.6	4.0	2.6				22.2	3.0	5.7				3.5	1.0	1.9
<i>Schinus molle</i>	6.5	2.0	3.4	13.9	2.0	10.0							7.0	1.0	3.6
<i>Sesbania punicea</i>	11.7	1.0	5.9				3.7	1.0	0.7						
<i>Tanuarix</i> spp.	2.6	1.0	1.3	5.6	1.0	3.6							1.8	1.0	1.0

F, % frequency of occurrence; A, mean abundance rating; P, prominence value; \* species occurring in the given category but not included in a formal recording in a road transect. Bold numbers: the highest prominence values in a given category which add up to ± 80% of the summed values (see text).

TABLE 9.—Alien species occurring in roadside and veld habitats in coastal renosterveld, coastal fynbos, mountain fynbos, mountain fynbos & forest of Fynbos Biome and study area

Biome and veld type category	Coastal renosterveld			Coastal fynbos			Fynbos Biome Mountain fynbos			Mountain fynbos & forest			Total			Total study area		
No. road transects	133			72			169			51			520			660		
	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P
<i>Acacia</i>																		
<i>baileyana</i>	0.8	1.0	0.2				4.7	2.0	0.9	2.0	1.0	0.3	1.9	2.0	0.4	1.5	2.0	0.2
<i>cyclops</i>	66.2	5.0	<b>51.0</b>	100.0	6.0	<b>89.5</b>	55.6	5.0	<b>35.9</b>	45.1	5.0	<b>20.9</b>	61.7	5.0	<b>52.8</b>	63.6	5.0	<b>45.2</b>
<i>dealbata</i>							3.6	2.0	1.2	2.0	1.0	0.3	1.3	3.0	0.5	1.1	3.0	0.3
<i>elata</i>	1.5	1.0	0.3				2.4	3.0	0.5	9.8	2.0	1.5	2.1	2.0	0.5	2.0	2.0	0.3
<i>longifolia</i>	9.8	5.0	<b>6.2</b>	20.8	5.0	<b>9.5</b>	27.2	4.0	<b>11.6</b>	13.7	3.0	4.4	15.6	4.0	<b>7.9</b>	12.6	4.0	<b>5.9</b>
<i>mearnsii</i>	58.6	4.0	<b>32.5</b>	4.2	3.0	1.2	59.2	5.0	<b>33.3</b>	100.0	6.0	<b>51.8</b>	48.5	2.0	<b>27.2</b>	52.9	5.0	<b>24.0</b>
<i>melanoxydon</i>	16.5	4.0	<b>9.2</b>				21.3	3.0	<b>5.2</b>	90.2	4.0	<b>28.0</b>	20.0	4.0	<b>8.0</b>	33.5	4.0	<b>10.8</b>
<i>podalyriifolia</i>	3.0	1.0	0.7	2.8	1.0	0.7	1.8	1.0	0.3	*			1.7	2.0	0.4	1.4	2.0	0.2
<i>pycnantha</i>	1.5	3.0	0.5	5.6	3.0	1.7	11.8	4.0	<b>4.2</b>	3.9	1.0	0.6	5.4	4.0	1.9	4.2	4.0	1.3
<i>saligna</i>	60.2	4.0	<b>30.7</b>	70.8	5.0	<b>38.8</b>	60.9	4.0	<b>28.1</b>	29.4	5.0	<b>11.2</b>	52.9	4.0	<b>28.0</b>	67.0	4.0	<b>24.8</b>
<i>Agave</i>																		
<i>americana</i>	5.3	1.0	1.2	8.3	2.0	2.2	2.4	1.0	0.5				5.8	2.0	1.4	9.4	2.0	1.5
<i>sisulana</i>	1.5	1.0	0.3				*						0.4	1.0	0.1	0.3	1.0	0.1
<i>Ailanthus altissima</i>				*			0.6	1.0	0.1	*			0.2	1.0	0.1	0.2	1.0	0.1
<i>Arundo donax</i>	3.8	2.0	0.9	*			0.6	1.0	0.1	3.9	1.0	0.6	1.5	2.0	0.4	6.5	2.0	0.9
<i>Atriplex nummularia</i>				*			0.6	2.0	0.1				1.0	2.0	0.2	11.7	2.0	1.7
<i>Bambusa balcooa</i>										*			*			*		
<i>Brugmansia</i> × <i>candida</i>	*									*			*			0.8	1.0	0.1
<i>Canna</i> sp.	*									*			*			*		
<i>Cereus jamacaru</i>	0.8	1.0	0.2										0.4	1.0	0.1	0.3	1.0	0.1
<i>Cestrum</i> cf. <i>laevigatum</i>	*												*			*		
<i>Cinnamomum camphora</i>	*												*			0.8	1.0	0.1
<i>Cortaderia selloana</i>	0.8	3.0	0.2				1.2	1.0	0.2	5.9	2.0	1.0	1.2	2.0	0.3	2.4	2.0	0.4
<i>Cupressus</i> cf. <i>arizonica</i>							0.6	1.0	0.1				0.2	1.0	0.1	0.2	1.0	0.1
<i>Cydonia oblonga</i>	0.8	1.0	0.2				0.6	1.0	0.1				0.4	2.0	0.1	0.3	2.0	0.1
<i>Echinopsis spachiana</i>																1.5	1.0	0.2
<i>Eriobotrya japonica</i>	*												*			*		
<i>Eucalyptus</i>																		
<i>camaldulensis</i>	2.3	2.0	0.6				1.2	2.0	0.3				1.0	2.0	0.2	3.8	2.0	0.6
<i>cladocalyx</i>	10.5	2.0	2.7	15.3	2.0	4.0	11.2	3.0	2.6	2.0	4.0	0.4	9.4	3.0	2.4	8.9	3.0	1.5
<i>diversicolor</i>	9.0	2.0	2.3	1.4	1.0	0.4	16.6	3.0	<b>4.0</b>	43.1	3.0	<b>8.7</b>	12.1	3.0	<b>3.4</b>	15.6	3.0	3.1
<i>ficifolia</i>							0.6	1.0	0.1				0.2	1.0	0.1	0.2	1.0	0.1
<i>globulus</i>	*						1.8	1.0	0.3	3.9	1.0	0.6	1.0	2.0	0.2	0.8	2.0	0.1
<i>gomphocephala</i>	0.8	4.0	0.3				1.8	3.0	0.5				1.0	4.0	0.3	0.8	4.0	0.2
<i>lehmannii</i>	9.8	2.0	2.5	29.2	4.0	<b>10.1</b>	12.4	4.0	<b>3.8</b>	2.0	1.0	0.3	10.8	4.0	<b>3.8</b>	8.5	4.0	2.5
<i>microcorys</i>										3.9	1.0	0.6	0.4	1.0	0.1	0.3	1.0	0.1
<i>regnans</i>	0.8	1.0	0.2				0.6	2.0	0.1				0.4	1.0	0.1	0.3	1.0	0.1
<i>spp.</i>	7.5	2.0	2.0	4.2	3.0	1.1	13.6	2.0	2.8	27.5	2.0	4.5	10.8	2.0	2.6	23.9	3.0	<b>3.8</b>
<i>Ficus carica</i>							*						0.4	1.0	0.1	5.6	1.0	0.8
<i>Fraxinus angustifolia</i>										2.0	1.0	0.3	0.2	1.0	0.1	2.4	1.0	0.3
<i>Gleditsia triacanthos</i>													0.2	2.0	0.1	0.2	2.0	0.1
<i>Grevillea robusta</i>																0.8	1.0	0.1
<i>Hakea</i>																		
<i>drupacea</i>	0.8	1.0	0.2	1.4	4.0	1.1	4.7	4.0	1.5				1.9	4.0	0.6	1.5	4.0	0.4
<i>gibbosa</i>				4.2	2.0	1.1	2.4	4.0	0.7				1.3	3.0	0.4	1.1	3.0	0.3
<i>sericea</i>	6.0	3.0	1.8	1.4	1.0	0.4	14.8	3.0	<b>4.1</b>	19.6	2.0	3.1	8.8	3.0	2.5	8.5	3.0	1.7
<i>Hedychium</i> sp.							*						*			*		
<i>Ipomoea</i> cf. <i>purpurea</i>	*						*						*			0.8	1.0	0.1
<i>Lantana camara</i>	3.0	2.0	0.7	1.4	1.0	0.4	0.6	1.0	0.1	2.0	1.0	0.3	1.3	1.0	0.3	1.1	1.0	0.2
<i>Lavatera arborea</i>	1.5	1.0	0.3	1.4	1.0	0.4	*						1.3	3.0	0.4	1.1	3.0	0.3
<i>Leptospermum laevigatum</i>	2.3	4.0	1.1	16.7	5.0	<b>7.1</b>	7.1	4.0	2.4	3.9	2.0	0.6	5.6	4.0	2.6	5.2	4.0	2.0
<i>Malus</i> sp.							*			2.0	1.0	0.3	0.2	1.0	0.1	0.2	1.0	0.1
<i>Melia azedarach</i>	4.5	1.0	1.1	2.8	1.0	0.7	5.9	1.0	1.1	2.0	1.0	0.3	3.7	1.0	0.9	5.2	1.0	0.8
<i>Metrosideros excelsa</i>							1.8	1.0	0.3				0.6	1.0	0.1	0.5	1.0	0.1
<i>Morus alba</i>				1.4	1.0	0.4							0.2	1.0	0.1	0.2	1.0	0.1
<i>Myoporum tenuifolium</i>	1.5	2.0	0.4	11.1	1.0	2.9	2.4	2.0	0.5				3.7	2.0	0.9	2.9	2.0	0.5
<i>Nerium oleander</i>																1.5	1.0	0.2
<i>Nicotiana glauca</i>	6.0	2.0	1.5	8.3	3.0	2.2	0.6	2.0	0.1				5.8	3.0	1.8	63.6	3.0	<b>9.7</b>
<i>Opuntia</i>																		
<i>ficus-indica</i>	29.3	3.0	<b>8.0</b>	19.4	2.0	5.1	16.0	2.0	3.5	13.7	2.0	2.2	22.1	3.0	<b>5.7</b>	71.5	3.0	<b>11.1</b>
<i>imbricata</i>	0.8	1.0	0.2										0.4	1.0	0.1	4.1	1.0	0.6
<i>microdasys</i>													*			*		
<i>robusta</i> cvs	1.5	1.0	0.3	*			0.6	1.0	0.1	2.0	1.0	0.3	1.0	1.0	0.2	10.9	1.0	1.6
<i>vulgaris</i>	0.8	4.0	0.3	2.8	1.0	0.7	1.8	1.0	0.3	3.9	1.0	0.6	1.5	2.0	0.4	2.7	2.0	0.4
<i>Paraserianthes lophantha</i>	4.5	2.0	1.1	8.3	4.0	2.2	15.4	3.0	3.6	19.6	3.0	4.1	9.2	3.0	2.6	7.3	3.0	1.6
<i>Passiflora</i>																		
<i>caerulea</i>	0.8	1.0	0.2										0.2	1.0	0.1	0.2	1.0	0.1
<i>edulis</i>	*												*			*		
<i>Pereskia aculeata</i>										2.0	1.0	0.3	0.2	1.0	0.1	0.2	1.0	0.1



TABLE 9 (cont.).—Alien species occurring in roadside and veld habitats in coastal renosterveld, coastal fynbos, mountain fynbos, mountain fynbos & forest of Fynbos Biome and study area

Biome and veld type category	Coastal renosterveld			Coastal fynbos			Fynbos Biome Mountain fynbos			Mountain fynbos and forest			Total			Total study area		
No. road transects	133			72			169			51			520			660		
	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P
<i>Phytolacca dioica</i>	0.8	2.0	0.2				1.2	1.0	0.2	2.0	1.0	0.3	0.8	2.0	0.2	1.4	2.0	0.2
<i>Pinus</i>																		
<i>cf. canariensis</i>	0.8	5.0	0.5				3.0	3.0	0.8				1.2	3.0	0.4	0.9	3.0	0.2
<i>halepensis</i>	1.5	1.0	0.3	4.2	2.0	1.1	13.0	2.0	2.7	3.9	3.0	0.7	6.5	2.0	1.6	5.2	2.0	0.9
<i>pinaster</i>	23.3	4.0	<b>10.3</b>	18.1	5.0	<b>7.2</b>	40.8	4.0	<b>16.5</b>	82.4	4.0	<b>22.2</b>	30.0	4.0	<b>12.7</b>	38.8	4.0	<b>12.0</b>
<i>pinea</i>	3.0	3.0	0.8	*			5.3	3.0	1.1				2.5	2.0	0.6	2.0	2.0	0.3
<i>radiata</i>	17.3	3.0	<b>5.0</b>	2.8	3.0	0.8	26.6	3.0	<b>7.1</b>	54.9	3.0	<b>10.7</b>	19.2	3.0	<b>5.5</b>	29.5	3.0	<b>5.8</b>
spp.	0.8	1.0	0.2				5.3	3.0	1.3				2.1	3.0	0.6	1.7	3.0	0.3
<i>Piptosporum undulatum</i>	1.5	2.0	0.3				0.6	1.0	0.1				0.6	3.0	0.1	0.5	3.0	0.1
<i>Platanus</i> sp.	*												*			*		
<i>Populus</i> × <i>canescens</i>	6.0	2.0	1.4	*			5.9	2.0	1.2	3.9	3.0	0.7	4.2	2.0	1.0	4.1	2.0	0.7
<i>Prosopis</i> spp.	7.5	3.0	1.7	2.8	2.0	0.7	3.0	3.0	0.7				4.4	3.0	1.2	5.3	3.0	0.9
<i>Prunus</i>																		
<i>armeniaca</i>							1.2	1.0	0.2				1.0	2.0	0.2	2.3	2.0	0.4
<i>persica</i>	10.5	1.0	2.5	2.8	1.0	0.7	8.3	2.0	1.6	5.9	1.0	0.9	7.5	2.0	1.7	9.7	2.0	1.5
<i>Psidium guajava</i>	0.8	1.0	0.2	2.8	2.0	0.7				2.0	1.0	0.3	0.8	2.0	0.2	0.6	2.0	0.1
<i>Punica granatum</i>	0.8	1.0	0.2				0.6	1.0	0.1				0.4	1.0	0.1	0.3	1.0	0.1
<i>Pyracantha angustifolia</i>	*						0.6	1.0	0.1				0.2	1.0	0.1	0.9	1.0	0.1
<i>Pyrus</i> sp.							0.6	2.0	0.1				0.6	2.0	0.1	0.5	2.0	0.1
<i>Quercus</i>																		
<i>robur</i>	5.3	3.0	1.4				4.1	2.0	0.9	5.9	2.0	0.9	3.3	2.0	0.8	3.3	2.0	0.5
spp.	0.8	2.0	0.2										0.2	1.0	0.1	0.2	1.0	0.1
<i>Ricinus communis</i>	17.3	2.0	<b>4.2</b>	13.9	3.0	3.8	5.9	1.0	1.2	5.9	3.0	1.0	9.6	2.0	2.3	25.0	2.0	<b>3.8</b>
<i>Robinia pseudoacacia</i>				*						*			*			0.8	1.0	0.1
<i>Rosa eglanteria</i>							1.8	3.0	0.4	2.0	1.0	0.3	0.8	2.0	0.2	0.6	2.0	0.1
<i>Rubus</i>																		
<i>flagellaris</i>							*			*			*			*		
<i>fruticosus</i>	13.5	3.0	<b>4.5</b>				21.3	3.0	<b>5.9</b>	39.2	4.0	<b>12.3</b>	14.6	4.0	<b>5.1</b>	17.9	3.0	<b>4.4</b>
<i>Schinus molle</i>	1.5	2.0	0.3	1.4	2.0	0.4	2.4	2.0	0.5				2.1	2.0	0.5	11.1	2.0	1.6
<i>Senna didymobotrya</i>	*												*			*		
<i>Sesbania punicea</i>	3.8	1.0	0.9	1.4	1.0	0.4	1.2	1.0	0.2	3.9	3.0	0.7	1.9	2.0	0.5	11.7	2.0	1.7
<i>Solanum mauritianum</i>	3.0	2.0	0.7				2.4	2.0	0.5	2.0	1.0	0.3	1.7	2.0	0.4	1.4	2.0	0.2
<i>Spartium junceum</i>	2.3	1.0	0.5	2.8	1.0	0.7	2.4	2.0	0.5				1.7	1.0	0.4	1.4	1.0	0.2
<i>Tamarix</i> spp.	0.8	1.0	0.2										0.4	1.0	0.1	5.6	1.0	0.8
<i>Vitis</i> cvs	*						2.4	2.0	0.5	2.0	1.0	0.3	1.0	2.0	0.2	0.8	2.0	0.1
<i>Wigandia caracasana</i>	0.8	1.0	0.2										0.2	1.0	0.1	0.2	1.0	0.1

F, % frequency of occurrence; A, mean abundance rating; P, prominence value; \* species occurring in the given category but not included in a formal recording in a road transect. Bold numbers: the highest prominence values in a given category which add up to ± 80% of the summed values (see text).

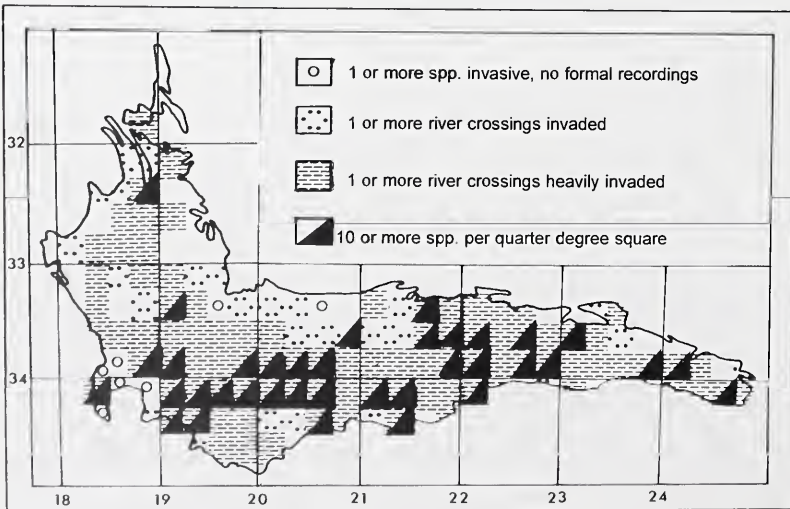


FIGURE 3.—Invasion in stream-bank habitats in terms of the intensity of invasion of watercourse crossings and species diversity per quarter degree square.

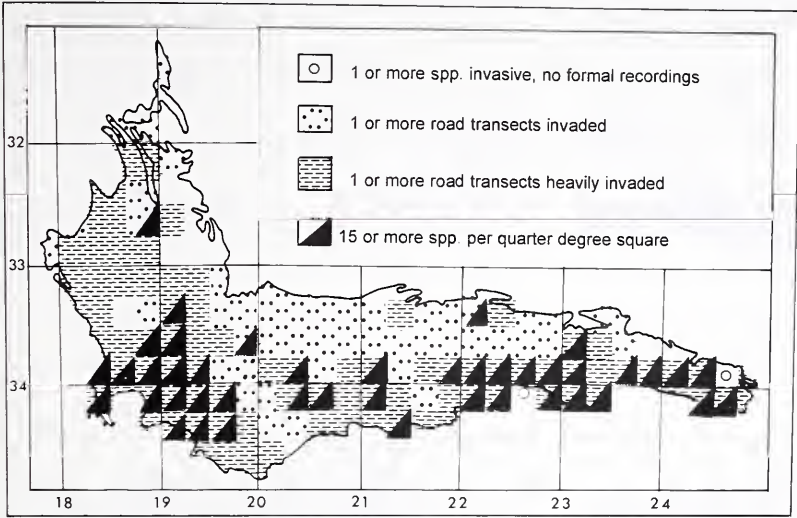


FIGURE 4.—Invasion in roadside and veld habitats in terms of the intensity of invasion of road transects and species diversity per quarter degree square.

exception of savanna. *Acacia mearnsii*, *A. saligna* and *A. cyclops* were the top three most prominent invaders with their combined prominence values amounting to 201 out of a total of 400 points for all species. In streambank habitats the *Acacia* species were dominant with five species (*A. mearnsii*, *A. saligna*, *A. cyclops*, *A. longifolia*, *A. melanoxylon*) amongst the top six most prominent species. In roadside and veld habitats four of the top six most prominent species were *Acacia* species (*A. cyclops*, *A. saligna*, *A. mearnsii* and *A. melanoxylon*).

*Acacia mearnsii* (Figure 6D) was a prominent invader in all vegetation categories with the exception of savanna, strandveld and coastal fynbos. It was recorded predominantly along watercourses and was the most prominent riverine invader in the Fynbos Biome and the whole study area. Unlike in Mpumalanga (of the former Transvaal) and KwaZulu-Natal, where it has been cultivated on a grand scale for tannin, it has been cultivated only on a small scale in the Cape, yet has spread widely. This is a reflection of its aggressiveness as an invader.

*Acacia saligna* (Figure 6G) was a prominent invader in all vegetation categories with the exception of savanna and forest. It was the next most prominent riverine invader in the study area after *A. mearnsii* and unlike *A. mearnsii* was prominent in strandveld and coastal fynbos. It was the second most prominent invader of roadsides and veld in the Fynbos Biome, after *A. cyclops*. Together with *A. cyclops* it formed extensive stands on the Cape Flats, where it was used for the stabilization of driftsands and was grown for tannin from 1850 until 1910 (Sturton 1978). It was most abundant in a broad band stretching from Bredasdorp northwestwards to Clanwilliam. It scored a highest abundance rating of 8 in the vicinity of Robberg (Plettenberg Bay) and Bredasdorp. A gall-forming rust fungus *Uromycladium tepperianum*, introduced for the biocontrol of *A. saligna* (Morris 1991), was only noted as abundant north of Cape Town between Atlantis and Kalkbaskraal in May 1993. Four years later, in 1997, it is abundant throughout the range of *A. saligna*.

*Acacia cyclops* (Figure 6A) was the most prominent invader in roadside and veld habitats in the Fynbos

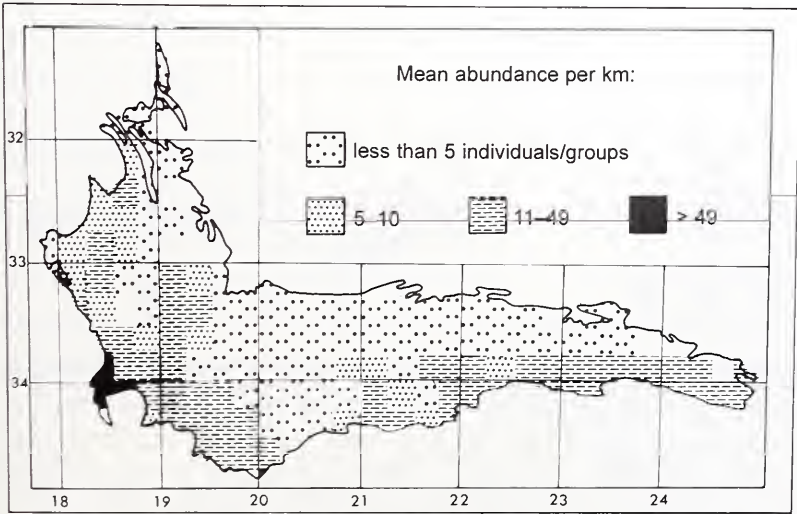


FIGURE 5.—Invasion in roadside and veld habitats in terms of the mean abundance of invaders per kilometre in each quarter degree square.

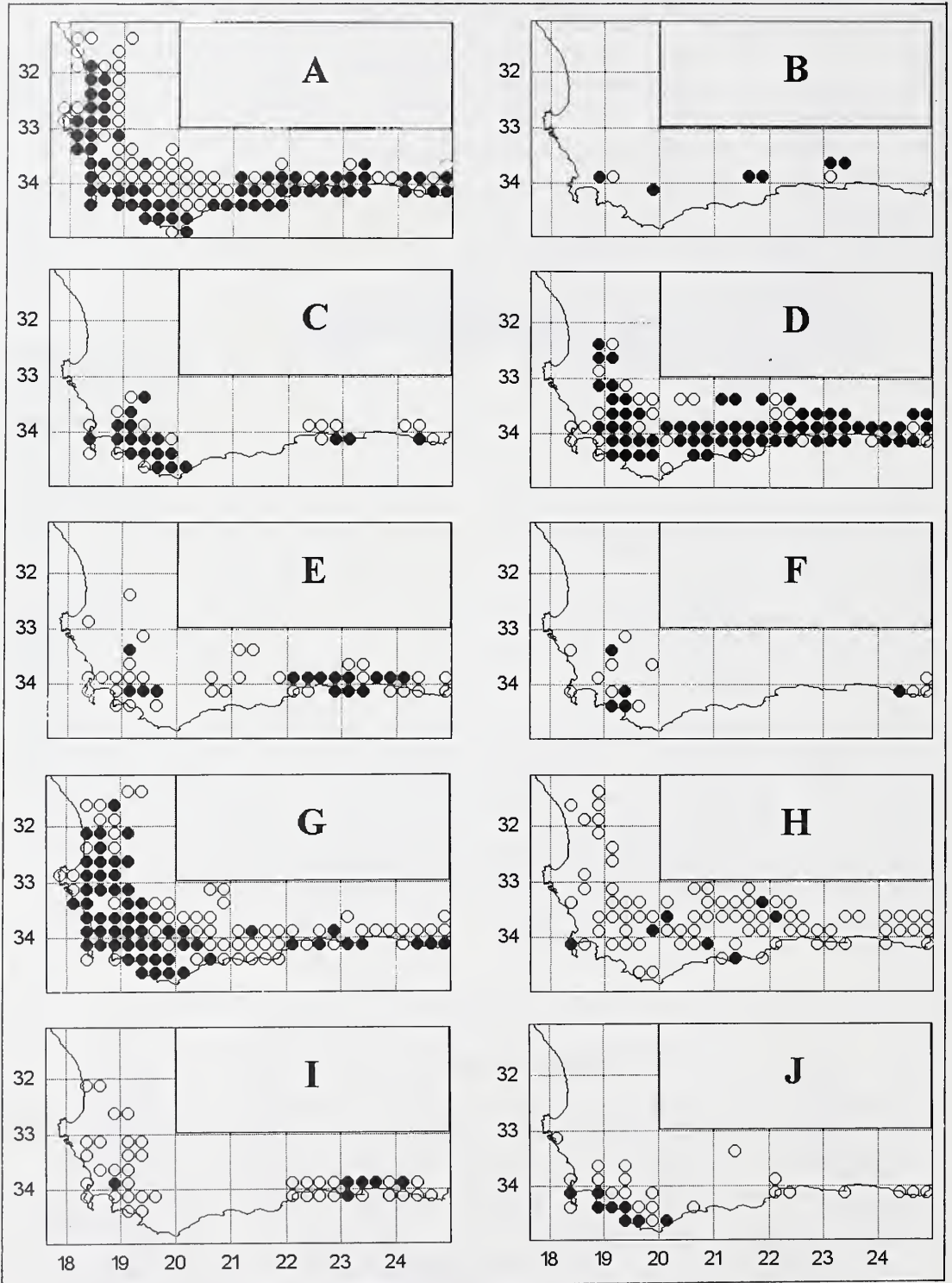


FIGURE 6.—Distribution of the most prominent species: A, *Acacia cyclops*; B, *A. dealbata*; C, *A. longifolia*; D, *A. mearnsii*; E, *A. melanoxylon*; F, *A. pycnantha*; G, *A. saligna*; H, *Arundo donax*; I, *Eucalyptus diversicolor*; J, *E. lehmannii*. Highest abundance rating of 4 or less, ○; highest abundance rating of 5 or more, ●.



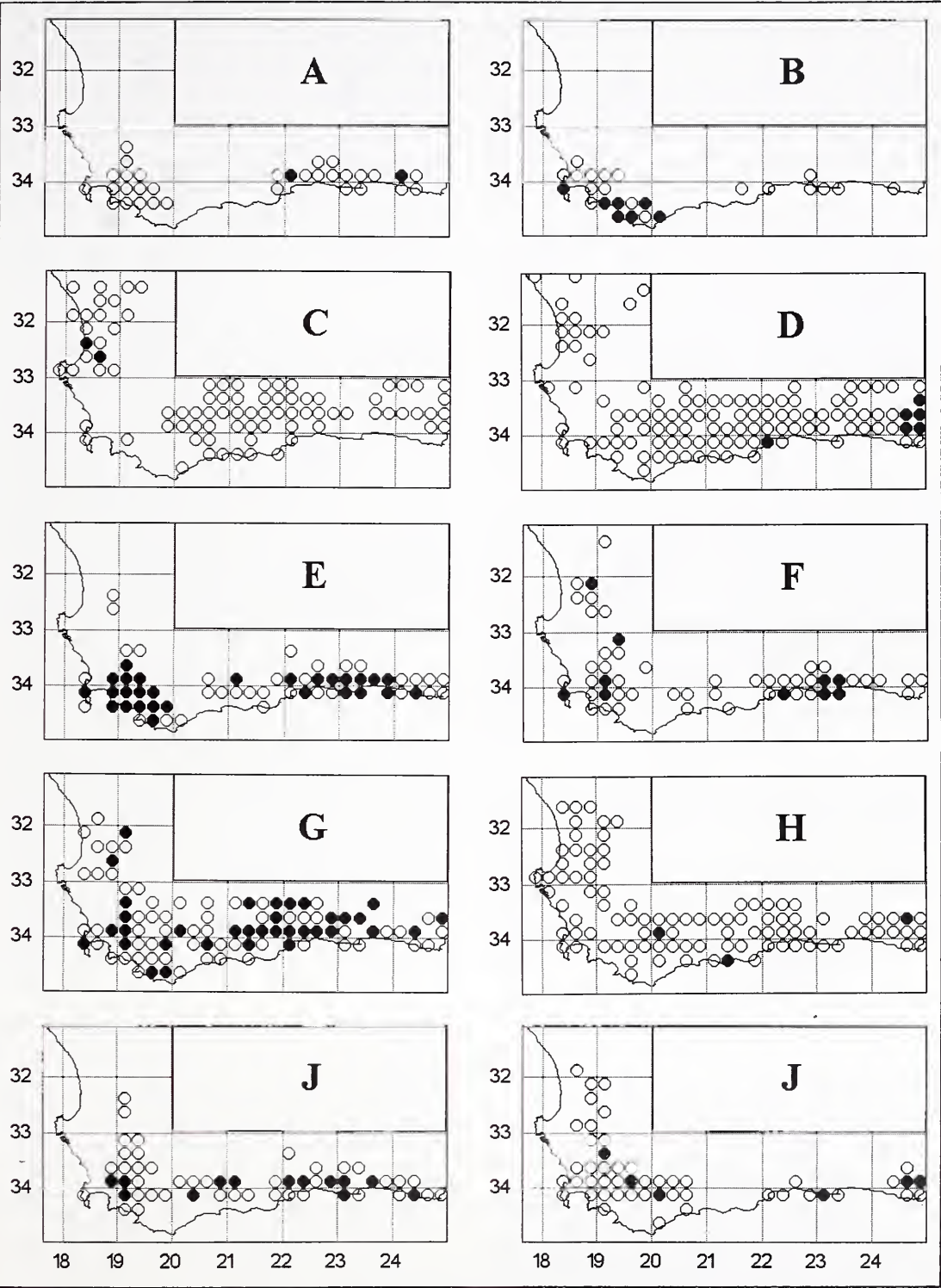


FIGURE 7.—Distribution of the most prominent species: A, *Hakea sericea*; B, *Leptospermum laevigatum*; C, *Nicotiana glauca*; D, *Opuntia ficus-indica*; E, *Pinus pinaster*; F, *P. radiata*; G, *Populus x canescens*; H, *Ricinus communis*; I, *Rubus fruticosus*; J, *Sesbania punicea*. Highest abundance rating of 4 or less, ○; highest abundance rating of 5 or more, ●.

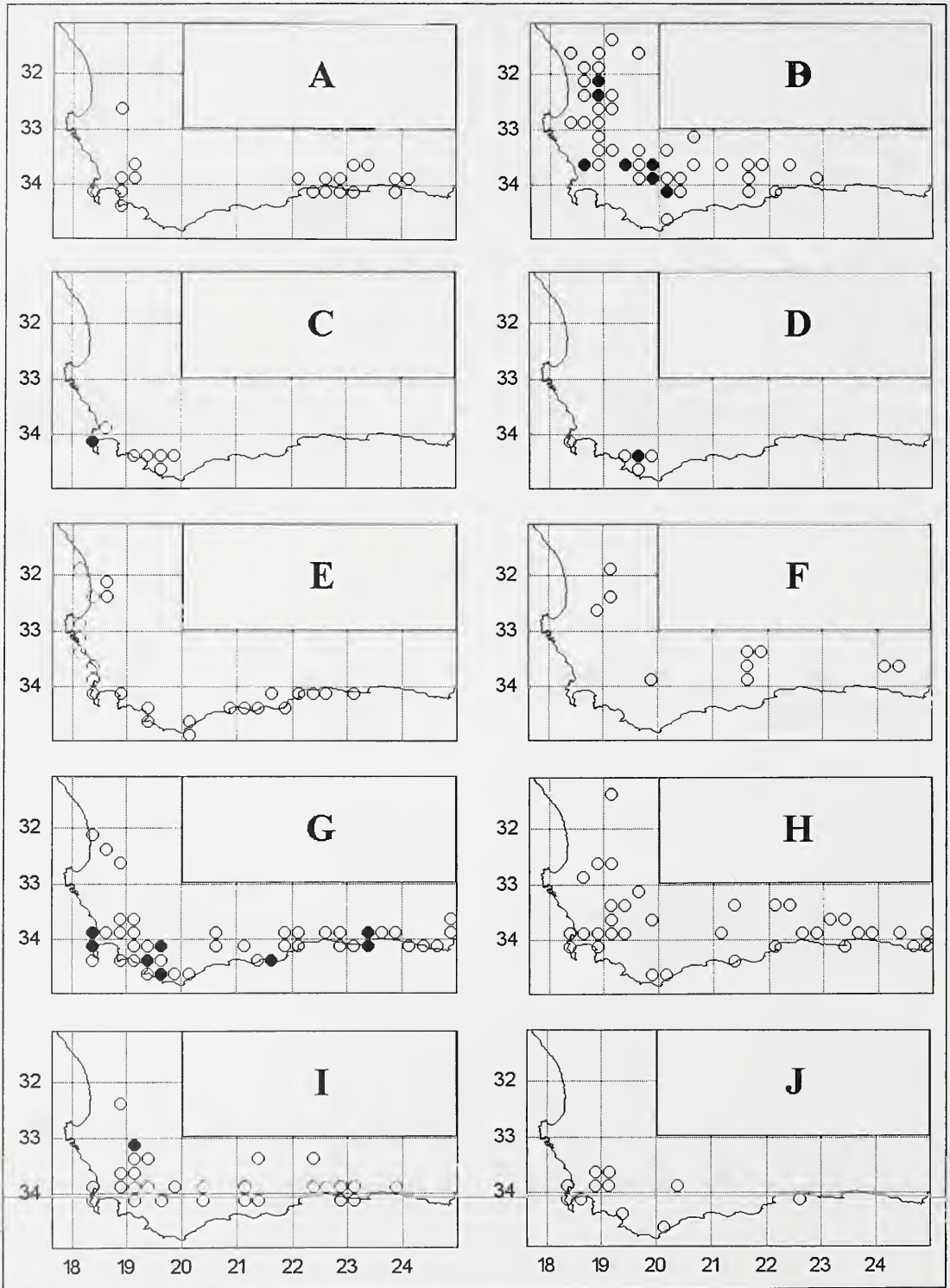


FIGURE 8—Distribution of less prominent and potentially important species: A, *Acacia elata*; B, *Eucalyptus cf. camaldulensis*; C, *Hakea drupacea*; D, *H. gibbosa*; E, *Myoporum tenuifolium*; F, *Nerium oleander*; G, *Paraserianthes lophantha*; H, *Pinus halepensis*; I, *Quercus robur*; J, *Spartium junceum*. Highest abundance rating of 4 or less, ○; highest abundance rating of 5 or more, ●.

Biome and in the whole study area. It was prominent along watercourses only in coastal fynbos. It formed very extensive stands on the Cape Flats, where it was established as a sand-binder from 1876–1886 (Stirton 1978). In the vicinity of Mitchell's Plain, Strandfontein and Muizenberg it formed almost pure stands for distances up to 10 km or more, thereby scoring the maximum abundance rating. It also scored the maximum rating in the vicinity of Cape Agulhas, Struisbaai and Quoin Point. It was exceedingly abundant (scoring an abundance rating of 7 or more) in coastal areas stretching all the way from Saldanha Bay in the west to Humansdorp in the east, a distance of approximately 1 000 km.

*Acacia melanoxylon* (Figure 6E) was concentrated in the forested area defined by the limits of Acocks's Veld Type 4, Knysna Forest. It was exceedingly abundant and the most prominent invader in the Forest Biome. The only other areas where it was recorded as abundant were in the vicinity of Wolseley and in the Riviersonderend Valley near Greyton. The abundance of this species around Knysna can be attributed to its use as a commercial timber tree and its consequent spread. It was used extensively from 1856 as a forest replacement species in the Knysna Forest, where it was planted in gaps created by the felling of indigenous trees (Stirton 1978). The indigenous forest pioneer tree, *Virgilia oroboides* was a widespread weed of roadsides and probably provides strong competition for *A. melanoxylon* and *A. mearnsii*.

*Acacia longifolia* (Figure 6C) was concentrated in a broad belt from Bredasdorp westwards to Cape Town and northwards as far as Ceres. Two other foci occurred eastwards around Knysna and Klipdrif, east of Storms River. It was absent from succulent karoo, savanna, strandveld and mountain renosterveld. In the remaining wetter vegetation categories, particularly coastal and mountain fynbos, it was more prominent in streambank habitats than roadside and veld habitats. Overall for the Fynbos Biome, it rated fifth and sixth most prominent in streambanks and roadsides/veld respectively. Galled plants, caused by the introduced wasp *Trichilogaster acaciaelongifoliae* for biocontrol (Dennill & Donnelly 1991), were very much in evidence throughout its distribution.

The biocontrol programme against *A. longifolia* has reduced seed production and the overall biomass of populations; in some instances it has caused mortality of adult trees (Dennill & Donnelly 1991). Now there also appears to be a reduction in the extent and abundance of this invader. Comparison of the distribution of *A. longifolia* in Richardson *et al.* (1992), which was based on reports from the mid 1980's, and with the present survey, shows a marked reduction in the extent and abundance of *A. longifolia* in the southern Cape.

*Acacia dealbata* (Figure 6B) was virtually restricted to watercourses in mountain fynbos. Although recorded at very few localities it was almost always abundant, forming dense stands. These localities were: Bergkloof River, near Herbertsdale; Uniondale Poort, Holdrif River; Riviersonderend; Dwaars River tributary, near Stellenbosch. *Acacia pycnantha* (Figure 6F) was restricted to the Fynbos Biome and was most prominent in road-

sides and veld habitats in mountain fynbos. It was exceedingly abundant i.e. scoring a 7 in the vicinity of Wolseley.

*Populus × canescens* (Figure 7G) was a widespread invader of watercourses and was recorded in all vegetation categories with the exception of the Forest Biome. It was the third most prominent riverine invader in the whole study area and in the Fynbos Biome.

*Pinus pinaster* (Figure 7E) was a prominent invader of mountain slopes in both the Forest and Fynbos Biomes. It has been used extensively for afforestation and its distribution is a reflection of planting patterns (Stirton 1978). *Pinus radiata* (Figure 7F) has been planted on a smaller scale and was less prominent than *P. pinaster*. These two species were the third and fourth most prominent invaders of roadside and veld habitats in the Forest Biome. They are the most prevalent species on the Cape Peninsula mountains (Moll & Trinder-Smith 1992).

*Rubus fruticosus* (Figure 7I) occurred mainly in the wetter vegetation types. It was most prominent in mountain fynbos & forest where it formed thickets along roadsides and on the margins of plantations or forest. In previous publications (Henderson 1989; Henderson 1992) reference was made to *R. affinis*. This is one of about 2 000 species belonging to the *Rubus fruticosus* complex (Tutin *et al.* 1968) and was regarded by Spies & Du Plessis (1985) to occur in South Africa. In this publication reference is made only to *R. fruticosus* L. aggregate which is in keeping with the Pretoria National Herbarium.

*Hakea sericea* (Figure 7A) was only rated tenth most prominent invader in mountain fynbos. This is an underestimate and resulted from the undersampling of mountain slopes. From a distance *Hakea* spp. are also more difficult to distinguish from the fynbos than for example the *Pinus* spp., which invade the same habitats. Richardson *et al.* (1992) gives a very different picture of the distribution and abundance of *H. sericea*, which they said occurred in 30% of the quarter degree squares in the Fynbos Biome and formed dense stands in 19% of squares. These records are based on Macdonald *et al.* (1985) but updated from various sources (D.M. Richardson pers. comm.).

*Eucalyptus* spp. were prominent invaders of the Forest Biome and mountain fynbos & forest. *E. diversicolor* (Figure 6I) has been cultivated commercially around Knysna and was the most prominent species in this region. It was often difficult to distinguish the *Eucalyptus* spp. and then they were recorded collectively. In the Knysna area it was not clear how abundant *E. cladocalyx* was. It was, however, regarded as one of the three problem species in the area, together with *E. diversicolor* and *E. microcorys* (forester at Woodville State Forest pers. comm.).

*Eucalyptus lehmannii* (Figure 6J) was the third most prominent invader in roadsides and veld habitats in coastal fynbos. It was most abundant in the coastal belt stretching from Bredasdorp westwards to the Cape



Peninsula. *E. cf. camaldulensis* (Figure 8B) was mainly an invader of watercourses and was most prominent in the Succulent Karoo Biome along the Breë River. It was also abundant along some watercourses in the Fynbos Biome, such as the Olifants River near Clanwilliam, Riviersonderend and Berg Rivers. *E. exserta*, which could be mistaken for *E. camaldulensis* was abundant on the Berg River near Langebaan and locally prominent on the Breë River near Robertson.

*Leptospermum laevigatum* (Figure 7B) was the sixth most prominent invader in roadside and veld habitats in coastal fynbos. It has been used mainly as a hedge or windbreak in coastal towns from where it has spread into the adjacent fynbos. It was most abundant on sandy soils from Bredasdorp westwards to Fish Hoek on the Cape Peninsula. It was exceedingly abundant around Hermanus and Kleinmond.

*Sesbania punicea* (Figure 7J) was recorded in all vegetation categories except savanna, strandveld and mountain renosterveld. It was most abundant along watercourses and in particular the Breë River in the Succulent Karoo Biome near Worcester. This species could have been underestimated in this survey as it is easily overlooked when not in flower.

*Opuntia ficus-indica* (Figure 7D) was by far the most widespread invader in the study area, being recorded in 71.5% of all road transects. It rated as the fifth most prominent invader in roadside and veld habitats in the study area but it was rarely abundant. It was only in the dry coastal bush around Mossel Bay that it scored an abundance rating of 5; elsewhere it occurred only as scattered individuals or small clumps.

*Nicotiana glauca* (Figure 7C) was the second most widespread invader, being recorded in 63.6% of all road transects. It was only recorded in disturbed sites such as along roads, railway lines, river banks, dry river beds, and in quarries and rubble heaps. It was a prominent invader of watercourses in the Succulent Karoo and Savanna Biomes but was never abundant. The only places where it was recorded as very abundant was on the roadside and floodplain adjacent to the Verlorevlei, north of Piketberg and near Elandsbaai.

*Arundo donax* (Figure 6H) was a widespread invader and was absent only from strandveld and forest. It was a prominent invader of watercourses in coastal renosterveld, succulent karoo and savanna. Flowering plants were only seen in the coastal belt near Humansdorp, Knysna and Wellington.

*Ricinus communis* (Figure 7H) was a widespread invader of roadside, veld and streambank habitats and was prominent in coastal renosterveld, savanna and succulent karoo. It was recorded in all vegetation categories but was only abundant in the Kogmanskloof near Montagu and in the Kafferkuilsrivier valley near Stilbaai.

*Agave americana* was prominent in succulent karoo and savanna but was never abundant. Its distribution is a reflection of where it has been planted. It appeared to have spread from seed in two localities within the succu-

lent karoo. These were north of Barrydale between the Anysberg and Warmwaterberg and in the Touws River valley south of Ladismith.

*Atriplex nummularia* was most frequently recorded in roadside and veld habitats in the succulent karoo, but it was never abundant. Judging from observations in the Great Karoo in the central Cape (Henderson in prep.) it is likely to become a prominent invader of seasonal and episodic watercourses in the succulent karoo of the Western Cape.

*Salix babylonica* was recorded along watercourses in all vegetation categories with the exception of strandveld. It was seldom abundant and its distribution was largely a reflection of where it has been planted. It was most prominent in mountain renosterveld where it was ranked third after *Acacia mearnsii* and *Populus × canescens*.

Species which scored abundance ratings of 5 or more but were not rated as prominent were: *Hakea gibbosa* and *H. drupacea* (= *H. suaveolens*), *Paraserianthes lophantha*, *Pinus cf. canariensis*, *Prosopis* spp. and *Lavatera arborea*. *Hakea gibbosa* (Figure 8D) was only recorded as abundant near Stanford on the Akkedisberg Pass. *H. drupacea* (Figure 8C) was only recorded as abundant on the Cape Peninsula between Simonstown and Smitswinkelbaai. If one compares the distributions of *H. gibbosa* and *H. drupacea* with those in Storton (1978) they appear to have changed little in the past twenty years.

*Paraserianthes lophantha* (Figure 8G) was most frequently recorded in mountain fynbos & forest and mountain fynbos. It has a preference for moist, low-lying sites. *Pinus cf. canariensis* was only recorded as abundant on dry mountain slopes near Paarl on the road to Franschoek. It was locally common around Ceres and Tulbagh. *Prosopis* spp. were only locally abundant on the plains to the east of Piketberg. They have been planted in this area and were just starting to spread as mostly small plants were seen along roadsides and along watercourses. *Lavatera arborea* was recorded along roadsides in many coastal towns; it was common to abundant near Saldanha Bay on the west coast.

Species that were only locally common (i.e. scoring abundance ratings of 4) were: *Tamarix* spp. along watercourses in succulent karoo and savanna near Oudtshoorn and in coastal renosterveld on the Gouritz River south of Mossel Bay; *Quercus robur* (Figure 8I) and *Quercus* spp. along watercourses near Stellenbosch and Swellendam; *Eucalyptus cladocalyx* and *E. gomphocephala* in several localities in mountain fynbos and coastal renosterveld; *Opuntia vulgaris* in coastal renosterveld near Mossel Bay; *Passiflora caerulea* along watercourses in coastal renosterveld near Riversdale; *Pinus pinea* in coastal renosterveld near Stellenbosch; and *P. halepensis* (Figure 8H) in mountain fynbos near Joubertina in the Lang Kloof. According to D.M. Richardson, pers. comm., *P. halepensis* has been underestimated in this study and it forms dense stands in the Jonkershoek Valley and on the Cape Peninsula near Miller's Point.

Several other species were locally common but were not included in formal recordings. These were: *Hedychium* sp., *Ipomoea* cf. *purpurea*, *Solanum mauritanum* and *Spartium junceum* on the Constantia Nek Road near Hout Bay on the Cape Peninsula. *Spartium junceum* (Figure 8J) was recorded in several localities, but mainly close to habitation and plantings. This species should be closely watched as it is showing signs of becoming invasive. *Phytolacca dioica* was locally common around Knysna.

*Metrosideros excelsa* is a potentially important invader of fynbos on moist, peaty soils. It was locally common at Betty's Bay where it has spread from plantings and threatens about three km of fynbos on the seafloor, but has been controlled at least since the early 1980's (R. Attwell pers. comm.). It has also spread from plantings around Hermanus (M.J. Wells pers. comm.). Small groups of naturalised plants were recorded on roadsides in the Cape Peninsula. These were on the Ou Kaapseweg, on the Steenberg; and on Boyes Drive between Muizenberg and Kalkbaai. In both cases they were in close proximity to suburban gardens and cultivated plants.

*Pittosporum undulatum* is a potentially important invader of fire-free, wooded or forested areas. It is a common hedge and ornamental garden plant in the Western Cape. In this survey it was seldom recorded as naturalised, but this could partly be due to its inconspicuousness in the habitats it invades. It was recorded in the river valley between Stellenbosch and Jonkershoek, and also on the Cape Peninsula on Boyes Drive at Kalk Bay. According to D.M. Richardson, pers. comm., it forms dense stands in the Jonkershoek State Forest and also at Newlands and Tokai State Forests on the Cape Peninsula. This species has become an important invader of forests in many parts of the world including Jamaica, New Zealand and even in Australia, where it is indigenous, but has invaded vegetation outside of its natural range (Gleadow & Ashton 1981). Recent reports of diseased plants caused by a pathogen in the Western Cape may help to curb the invasiveness of *P. undulatum* in South Africa (M.J. Morris pers. comm.).

*Myoporum tenuifolium* (Figure 8E), a tree with somewhat succulent leaves and adapted to windy, salt-laden air, has been planted as a windbreak and for shade in all coastal towns in the study area. Occasional seedling spread was recorded throughout its range but was most noticeable in strandveld from the Cape Peninsula northwards to the west coast. It appeared to be better adapted to the more arid and semisucculence of the strandveld rather than coastal fynbos.

*Nerium oleander* (Figure 8F) has invaded watercourses in dry mountain valleys in several parts of the study area. It was most evident along the Gamka, Huis and Gouritz Rivers in the Ladismith and Calitzdorp Districts. It was also recorded near Robertson along the Breë River, at Citrusdal through the Piekenierskloof (Grey's Pass), and at Wuppertal on the Tra-Tra River. It is known to occur in the Cederberg (Stirton 1978) but this region was not surveyed due to bad weather conditions at the time.

*Acacia elata* (Figure 8A) was most frequently recorded in the mountain fynbos & forest and forest vegetation categories. Virtually all recordings were of seedling spread from plantings in urban areas or close to habitation. On a few occasions, however, seedlings were noted on roadsides far from any plantings e.g. on the Franschhoek and Du Toits Kloof Passes.

### Relation of invasion to historical and environmental factors

Alien plant invasion in the southern and southwestern Cape has been greatly influenced by the deliberate introduction and large scale planting of alien plant species which were adapted to the prevailing environmental conditions. For the first 150 years after the colonisation of the Cape in 1652, plants of mainly European origin were introduced. Only a few of these plants have become invasive such as *Pinus pinaster* a native of the Mediterranean and adapted to the climate and soils of the southern Cape. It was only after 1830, when tree and shrub species were intentionally imported from areas of similar climate, especially southern and western Australia, and were extensively propagated, that most of the important invaders of natural vegetation became established (Richardson *et al.* 1992).

By 1865 all of the most prominent *Acacia*, *Hakea* and *Pinus* species mentioned in this survey, had been introduced to the Cape Town region (McGibbon 1858; Shaugnessy 1986). The government forestry authority played a major role in attempting to establish many of these plants both on the Cape Flats and on Table Mountain and adjoining mountains (Shaugnessy 1986). They also encouraged private growers to establish alien plantations. The reasons for the plantings were various: timber, fuel, shelter, driftsand stabilisation, tannin production and simply beautification of a landscape that was perceived at the time to be 'bleak and naked' (Shaugnessy 1986). Forestry officials even justified the afforestation of Table Mountain in terms of improved water supply and fire control (Shaugnessy 1986) which is exactly opposite to today's thinking.

In the southern Cape forests, fast-growing alien trees, particularly *Acacia*, *Eucalyptus*, *Pinus* and *Quercus* species, were planted in forest gaps and in plantations along the margins of forests. *Acacia melanoxylon*, the most prominent invader in the forested areas of the southern Cape today, occurred as large trees around George and Knysna by 1876 (Geldenhuys *et al.* 1986).

The pattern of invasion of several of the most widespread species today, such as *Pinus pinaster*, *Acacia cyclops* and *A. saligna* is a reflection of where they were planted. The disturbance of the soil and destruction of indigenous vegetation when establishing plantations of these alien species would have created conditions favourable for their further spread and also for the spread of other alien species. Later the abandonment of many of the plantations left stands of aliens which could act as a seed source for future generations of these species (Shaugnessy 1986).



Successful invaders in the Fynbos Biome have to be either tolerant of, or adapted to, nutrient-poor sandy soils and periodic high-intensity fires, particularly in mountain fynbos. Fire may encourage invasion by activating mass seed release from serotinous cones (as in *Hakea sericea* and *Pinus pinaster*), and by stimulating germination of soil-stored seeds as in *Acacia saligna* and *A. longifolia* (Richardson *et al.* 1992). The aforementioned *Acacia* species show a further adaptation which enables their seeds to avoid destruction by fire on the soil surface. Their seeds, with fleshy attachments that are eaten by ants, are buried in caches below the soil surface (Dean *et al.* 1986). *A. saligna* also has the ability to coppice after fire.

The Fynbos Biome is subjected to strong winds throughout the year and this has facilitated the rapid spread of species with winged seeds, mainly those of the *Hakea* and *Pinus* species. Whereas seed dispersal in mountain fynbos is mainly by wind and water; in the lowlands birds, mammals (including humans and their implements), ants and water are important. For example, *Acacia cyclops* seed is dispersed by mammals, such as the striped field mouse and the chacma baboon (Stirton 1978), and many indigenous birds as well as the introduced European starling (Glyphis *et al.* 1981). The large seeds of *Pinus pinea* are dispersed by the grey squirrel (Richardson *et al.* 1994).

Watercourses have played an important role in the long-range dispersal of alien plants throughout the study area. Species that have depended mainly on water dispersal include the hard-seeded legumes which are not bird- or ant-dispersed and are otherwise relatively immobile such as *Acacia dealbata*, *A. mearnsii*, *Paraserianthes lophantha* and *Sesbania punicea*. Watercourses have also enabled some species, for example, *A. saligna* and *A. mearnsii*, to penetrate the dry interior of the Succulent Karoo and Savanna Biomes. *Nerium oleander* is confined to riverbeds and is dependant on moisture for the germination and survival of its seedlings.

#### SOME IDEAS FOR THE FUTURE

Since this survey was completed in 1993, a national programme for the removal of alien plant invaders in the water catchments of South Africa has been initiated. The project is government-aided and is called the *Working for Water* Programme of the Department of Water Affairs and Forestry. The 1997/98 budget stands at R115 million and the prospects for further funding are promising (Preston 1997). It is envisaged that a large proportion of the funds will be derived from water levies which are likely to become a long-term source of funding (H.G. Zimmermann pers. comm.). The proposed 'interception of water levy' is aimed primarily at the forestry industry which is one of the major water users in the country (Yeld 1997). Clearing operations were started in October 1995 and by the end of March 1997, 71 289 hectares had been cleared (Willems 1997). However the ultimate success of the project will depend on very strict follow-up operations over an extended period of time. If these conditions are not met then the problem could be exacerbated rather than improved.

Many of the problem species are also useful plants and several are major commercial forestry crops. There is a growing call for instituting the 'polluter pays' principle, whereby the parties that benefit through the propagation of these species must contribute to the costs of controlling their spread from sites of propagation (Ivey & Heydenrych 1995; Richardson *et al.* 1997; Yeld 1997).

Prevention is better than cure! Every attempt should be made to prevent other, new species from becoming invasive. The possibility of developing sterile cultivars of commercially important species needs investigating. The most important step should be the screening of alien plant species for potential invasiveness before they are introduced and widely planted. To this end, an expert system has been developed to assist authorities in screening plants for their invasive potential (Tucker & Richardson 1995).

Biological control using mainly introduced insects and pathogens could play an increasingly important role in the long-term and sustainable control of invasive plant species in the study area. Some programmes have already been so successful, especially those against *Acacia saligna* and *A. longifolia*, that they could ultimately lead to the destruction of all the dense infestations of these species and severely restrict any further spread.

This paper has focused on woody plants which are the most prominent invaders of fynbos. However herbaceous alien plants are also important in some systems (Vlok 1988). There is an urgent need to assess the extent of invasions by alien herbs, especially in the remaining vegetation on the lowlands, and to determine what impacts they are having.

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## APPENDIX

The names of 136 species of naturalised alien trees, shrubs and climbers are listed. Some non-woody species are included. Names and dates in brackets indicate literature references. (PRE): cited on Pretoria National Herbarium specimen labels.

### Acacia

*baileyana* F.Muell., Bailey's wattle  
*culturiformis* A.Cunn. (Buys *et al.* 1991), knife-leaved wattle  
*cyclops* A.Cunn. ex G.Don, red eye/rooikrans  
*dealbata* Link, silver wattle  
*elata* A.Cunn. ex Benth., peppertree wattle

*implexa* Benth. (Buys *et al.* 1991), screw-pod wattle  
*longifolia* (Andr.) Willd., long-leaved wattle  
*mearnsii* De Wild., black wattle  
*melanoxylon* R.Br., Australian blackwood  
*podalyriifolia* A.Cunn., pearl acacia  
*pycnantha* Benth., golden wattle

- Acacia* cont.  
*saligna* (Labill.) H.L. Wendl., Port Jackson willow  
*viscidula* A.Cunn. ex Benth. (Moll & Scott 1981)
- Agave*  
*americana* L., American agave  
*sisalana* Perrine, sisal
- Ageratina adenophora* (Spreng.) R.M. King & H. Rob. (Buys *et al.* 1991), crofton weed
- Ailanthus altissima* (Mill.) Swingle, tree-of-heaven
- Alhagi maurorum* Medik. (= *A. camelorum* Fisch.) (PRE), camelthorn bush
- Alnus glutinosa* (L.) Gaertn. (Moll & Scott 1981), black alder
- Anredera baselloides* (Kunth) Baill. (Buys *et al.* 1991), bridal wreath
- Araujia sericifera* Brot. (Bond & Goldblatt 1984), moth catcher
- Arundo donax* L., giant reed
- Atriplex nummularia* Lindl. subsp. *nummularia*, old man's salt bush
- Bambusa balcooa* Roxb. ex Roxb., common bamboo
- Bambuseae sp., small unidentified bamboo
- Brugmansia × candida* Pers. [= *Datura × candida* (Pers.) Saff.], angel's trumpet
- Callistemon rigidus* R.Br. (Macdonald *et al.* 1987), Australian bottlebrush
- Canna indica* L. (Adamson & Salter 1950), canna
- Cardiospermum grandiflorum* Sw. (Buys *et al.* 1991), balloon vine
- Castanea dentata* (Marshall) Borkh. (Moll & Scott 1981), American chestnut
- Casuarina* sp., beefwood tree
- Cereus jamacaru* DC. [*C. peruvianus* (L.) Mill. misapplied in SA], queen of the night
- Cestrum* cf. *laevigatum* Schldl., inkberry
- Cinnamomum camphora* (L.) J. Presl, camphor tree
- Colocasia* cf. *esculenta* (L.) Schott, taro
- Cortaderia selloana* (Schult.) Asch. & Graebn., Pampas grass
- Cupressus*  
 cf. *arizonica* Greene, Arizona cypress  
*macrocarpa* Hartw. (Macdonald *et al.* 1987), black cypress
- Cydonia oblonga* Mill., quince
- Cytisus*  
*monspessulanus* L. [= *C. candicans* (L.) Lam. (Buys *et al.* 1991)], Montpellier broom  
*scoparius* L. (Buys *et al.* 1991), Scotch broom
- Echinopsis spachiana* (Lem.) Friedr. & Rowley [= *Trichocereus spachianus* (Lem.) Riccob.], torch cactus
- Eriobotrya japonica* (Thunb.) Lindl., loquat
- Eucalyptus*  
*camaldulensis* Dehnh., red river gum  
*cladocalyx* F.Muell., sugar gum  
*diversicolor* F.Muell., karri  
*exserta* F.Muell.  
*ficifolia* F.Muell., red flowering gum  
*globulus* Labill., blue gum  
*gomphocephala* A. DC., tuart  
*lehmannii* (Schauer) Benth., spider gum  
*leucoxydon* F.Muell., white ironbark  
*microcorys* F.Muell., tallow gum  
*regnans* F.Muell., giant gum  
*sideroxylon* A.Cunn. ex Wools (Macdonald *et al.* 1987), black ironbark
- Ficus carica* L., edible fig
- Fraxinus angustifolia* Vahl, Algerian ash
- Gleditsia triacanthos* L., honey locust
- Grevillea robusta* A.Cunn., Australian silky oak
- Hakea*  
*drupacea* (Gaertn.f.) Roem. & Schult. (= *H. suaveolens* R.Br.), sweet hakea  
*gibbosa* (Sm.) Cav., rock hakea  
*sericea* Schrad., silky hakea
- Hedychium coronarium* J.König (Adamson & Salter 1950), white ginger lily
- Hypericum perforatum* L. (Buys *et al.* 1991), St John's wort
- Ipomoea*  
*nil* (L.) Roth.  
*purpurea* (L.) Roth. (Bond & Goldblatt 1984), morning glory
- Lantana camara* L., lantana
- Lavatera*  
*arborea* L., tree mallow  
*cretica* L. (Moll & Scott 1981)
- Leptospermum laevigatum* (Gaertn.) F.Muell., Australian myrtle
- Ligustrum*  
*japonicum* Thunb. (Adamson & Salter 1950), Japanese wax-leaved privet  
*sinense* Lour. (Adamson & Salter 1950), Chinese privet
- Malus* sp., apple tree
- Melia azedarach* L., syringa or Persian lilac
- Metrosideros excelsa* Sol. ex Gaertn., New Zealand bottlebrush
- Morus alba* L., white mulberry
- Myoporum tenuifolium* Forst.f. subsp. *montanum* (R.Br.) Chinnock (*M. acuminatum* R.Br. misapplied in SA), manatoka
- Nerium oleander* L., oleander
- Nicotiana glauca* Graham, wild tobacco
- Opuntia*  
*ficus-indica* (L.) Mill., sweet prickly pear  
*imbricata* (Haw.) DC., imbricate prickly pear  
*microdasys* (Lehm.) Pfeiff., bunny-ears  
*robusta* cvs, spineless prickly pears  
*vulgaris* Mill., cochineal prickly pear
- Paraserianthes lophantha* (Willd.) Nielsen subsp. *lophantha* [= *Albizia lophantha* (Willd.) Benth.], stink bean
- Passiflora*  
*caerulea* L., blue passion flower  
*edulis* Sims, purple granadilla  
*molissima* (Kunth) L.H. Bailey (Macdonald 1987), banana poka  
 cf. *quadrangularis* L. (McDonald & Morley 1988), giant granadilla
- Pereskia aculeata* Mill., Barbados gooseberry
- Phoenix*  
*canariensis* Hort. ex Chabaud, Canary date palm  
*dactylifera* L., real date palm  
 sp. (Moll & Scott 1981), palm
- Phytolacca dioica* L., belhambra
- Pinus*  
 cf. *canariensis* Sweet ex Spreng., Canary pine  
*halepensis* Mill., Aleppo pine  
*pinaster* Aiton, cluster pine  
*pinet* L., umbrella pine  
*radiata* D. Don, radiata pine
- Pittosporum undulatum* Vent., Australian cheesewood
- Platanus* sp., plane tree
- Populus*  
 × *canescens* (Aiton) Sm., grey poplar  
*deltoides* W. Bartram ex Marshall, match poplar  
*nigra* L. 'italica', Lombardy poplar
- Prosopis* spp., mesquite trees
- Prunus*  
*armeniaca* L., apricot  
*persica* (L.) Batsch, peach
- Psidium guajava* L., guava
- Punica granatum* L., pomegranate
- Pyracantha angustifolia* (Franch.) C.K. Schneid., yellow firethorn
- Pyrus* sp., pear tree
- Quercus*  
*canariensis* Willd. (= *Q. mirbeckii* Durieu) (Moll & Scott 1981), Algerian oak  
*cerris* L. (Moll & Scott 1981), Turkey oak  
*palustris* Münchh. (Moll & Scott 1981), pin oak  
*robur* L., English oak  
*suber* L. (Moll & Scott 1981), cork oak
- Ricinus communis* L., castor-oil plant
- Robinia pseudoacacia* L., black locust
- Rosa eglanteria* L., eglantine
- Rubus*  
*flagellaris* Willd.  
*fruticosus* L. agg., European blackberry; this includes *R. affinis* Weihe & Nees according to Spies & Du Plessis (1985)  
*rosifolius* Sm. (Moll & Scott 1981)
- Salix*  
*babylonica* L., weeping willow  
*caprea* L. (Moll & Scott 1981), pussy willow  
 cf. *fragilis* L., crack willow
- Schinus molle* L., pepper tree
- Senna didymobotrya* (Fresen.) Irwin & Barneby (= *Cassia didymobotrya* Fresen.), peanut butter cassia
- Sesbania punicea* (Cav.) Benth., red sesbania
- Solanum*  
*hermannii* Dunal (Bond & Goldblatt 1984), bitter apple  
*mauritanum* Scop., bugweed
- Spartium junceum* L., Spanish broom
- Tamarix*  
*ramosissima* Ledeb. (PRE), pink tamarisk  
 spp., tamarisks
- Tetraclinis articulata* (Vahl) Mast. (Rourke 1991), arar tree
- Vitis* cultivars, grapes
- Wigandia caracasana* Kunth



## Miscellaneous notes

### NEW EDITOR FOR *BOTHALIA*

The first volume of *Bothalia*, house journal of the National Botanical Institute (NBI) of South Africa, was published in 1921. It was produced by the Division of Botany and Plant Pathology, Department of Agriculture, Pretoria, one of the precursors of the NBI. Dr I.B. Pole Evans (Figure 1), the initiator of *Bothalia*, named the journal after the late General Louis Botha, 'in view of the great agricultural development which has taken place in South Africa, since Union, and bearing in mind that much of this was due to the policy and influence of the first Union Premier and Minister for Agriculture' (preface to *Bothalia* 1: 1, 1921). Since its inception the journal has published scientific papers mainly in the fields of plant taxonomy/systematics and ecology, focusing primarily on the rich southern African flora.

The editorial policy of *Bothalia* has throughout been one of maintaining and promoting excellence in scientific publishing. This is reflected in, amongst others, the maintenance for many years of a high Impact Factor, as measured by the ISI Citation Index. This factor is calculated from the number of times that an article is cited from *Bothalia* in a given year.

From its first appearance in 1921, until June 1997, *Bothalia* has had five editors. They were: Drs I.B. Pole Evans (1921–1939) (Figure 1); R.A. Dyer (1941–1957)



FIGURE 1.—I.B. Pole Evans, editor from 1921–1939.



FIGURE 2.—R.A. Dyer, editor from 1941–1957.

(Figure 2); L.E. Codd (1958–1974) (Figure 3); D.J.B. Killick (May 1975–1985) (Figure 4); and O.A. Leistner (Figure 5), who served as editor from 1986 until his retirement from this post in June 1997. It was recently announced that Mr Gerrit Germishuizen (Figure 6) will fill this position from 1 July 1997. Mr Germishuizen has worked at the NBI for more than 21 years. He started out as Professional Officer in Wing B (Phillips Wing) of the National Herbarium during 1975, where he curated and identified members of the Fabaceae, Polygonaceae, Loranthaceae and Viscaceae. In 1994 he was appointed Assistant Curator: Finance for the herbarium. His lengthy association with the artist Anita Fabian has led to the publication of the books *Transvaal wild flowers* in 1982 and *Wild flowers of northern South Africa* in 1997. To date he has more than 70 publications to his credit.

On behalf of the contributors to and readership of *Bothalia*, Gerrit is wished well with his venture into this new field. Together with the rest of the staff of the Scientific Publications Unit of the NBI, Mmes Henriette du Plessis (Head), Emsie du Plessis (Technical Editor), Bev Momberg (Technical Editor), Sarie Brink (Chief Typesetter), and Daleen Maree (Senior Typist) he will be





FIGURE 3—L.E. Codd, editor from 1958–1974.



FIGURE 4—D.J.B. Killick, editor from 1975–1985.



FIGURE 5—O.A. Leistner, editor from 1986 to June 1997.



FIGURE 6.—G. Germishuizen.

called upon to maintain and improve the scientific value and impact of *Bothalia* and the Institute's other publications.

Dr Leistner has been appointed on a contract to edit *Families and genera of southern African seed plants*. It is

anticipated that this single volume update of R.A. Dyer's *Families and genera of southern African flowering plants* will be published in 1999.

G. F. SMITH  
Director: Research





## OBITUARIES

JOHN DENZIL CARR (1916–1997)

Denzil Carr (he seldom used his first given name, John) (Figure 1) was born in Germiston, Transvaal, on 12 November 1916. He read electrical engineering at the University of the Witwatersrand between 1936 and 1940, graduating B.Sc.Eng. He served as a bomber pilot with 21 Squadron SAAF, during World War II, whereafter he was transferred to SA Signals Corps. After the war, he lived in Sale, then part of Cheshire, now part of the southwestern fringe of Greater Manchester. It was at this time that he met Dorothy Ann Buxton, secretary of the local art society. After several years he returned to South Africa, and was then employed in the mining industry. Once he was established in a good position with Anglovaal Mining Corporation, he wrote to Dorothy offering her a job as his wife!—they were married on 13 August 1948.

When exactly the Carrs joined the Tree Society of southern Africa is not clear; Balkwill (1996) suggests 1949 or 1950; Dorothy was always adamant that it was 1954. However, the biography on the dust-jacket of his *Acacia* book (Carr 1976) suggests 1956. Seeing that the Society's records of that period have vanished, the correct date may never be known. Be that as it may, in due course the Carrs were absorbed into the running of the Society. Denzil was elected chairman, and Dorothy treasurer of the Society in 1965 (Rasmussen 1965). At that stage the Society's funds on hand amounted to the princely sum of 50c, but Dorothy took matters in hand and soon the financial situation was much healthier.

In 1976 Ken Cunliff, who had edited the Society's journal, *Trees in South Africa*, for many years, died, and Denzil took up that task as a matter of course. However, the two posts in the Society were too much for one person, so at the 1977 AGM he resigned the chairmanship. He continued to edit the journal until 1995, though with limited assistance from other members during the latter years. In 1994 he was elected President of the Society, but failing health compelled him to stand down from this office one year later.

Denzil's interest in trees was sparked off by a visit in his youth to the Lowveld, which at the time was largely unspoilt. Whatever he did was thoroughly done, and so he was not satisfied merely to attend Society outings and serve on a committee—he started to amass detailed practical information on growing trees from seed on his property in Morningside, Sandton, and he wrote articles on every aspect of an amateur's involvement with trees for the Society's journal. Only Ken Cunliff, with his quarterly column 'Trees for Tomorrow', was a more prolific writer. Denzil's field knowledge of trees also led to longer publications: *The South African Acacias*, Johannesburg 1976, and *Combretaceae in southern Africa*, Johannesburg 1988. His studies of tree propagation resulted in his last book, *The propagation and cultivation*

*of indigenous trees and shrubs on the highveld*, Sandton 1994. His *Acacia* and *Combretum* books, and many editions of *Trees in South Africa* are graced by his pencil drawings and photographs (Figure 2). Of his books, the first is now Africana and not readily available, but the latter two are still in print.

He was also chairman of the Sandton Nature Conservation Society for several years from 1972. In 1993 the Botanical Society of South Africa awarded him the Marloth Medal for his work on *Acacia* and *Combretaceae*. This was only the third time this medal had been awarded since its inception in 1987. It is presented in recognition of the promotion of the indigenous flora of southern Africa by means of significant publications written by non-botanists. The name of the medal honours Rudolf Marloth (1855–1931), an analytical chemist and botanist who wrote the beautifully illustrated multi-volume *Flora of South Africa*.

Denzil's last years became an increasing burden to him since failing health took its toll, first on his mobility and then on his other faculties. He died at his son Richard's home at Tygerpoort, east of Pretoria on 29 August 1997, during the early hours of the morning. He leaves two sons and two grandchildren.



FIGURE 1.—John Denzil Carr (1916–1997).



FIGURE 2.—Flowering branch of *Acacia sieberiana*, drawn by Denzil Carr in his book, *The South African Acacias* (1976).

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H.F. GLEN

#### HERMANUS PHILLIPUS VAN DER SCHIJFF (1921–1997)

Prof. Manie (Figure 3), as he was known to his friends and many of his colleagues, will be remembered as the first biologist appointed in the Kruger National Park and for laying the foundation for the scientific management of the Park. He will also be remembered for his enthusiasm, dedication and discipline that inspired so many students to further their studies in ecology, plant morphology and plant taxonomy. Prof. Manie was always there to lend a hand and to assist. I shall remember him as a person who was only satisfied with the best and he never accepted 'no' for an answer. Due to his intense interest in his students he always inspired them to deliver their best by working hard and by using their time profitably. He believed in set hours and expected to find postgraduate students diligently at work in the laboratories or in their offices after hours, without, however, sacrificing their social life. The example he set on field excursions was always stimulating and a wonderful learning experience.

Hermanus Phillipus van der Schijff was born on 18 August 1921 on the Farm Sterkstroom in the Ventersdorp District in the North-West (Western Transvaal). He attended the Sterkstroom West Primary School and after matriculating from the Ventersdorp Secondary School in 1941, he furthered his studies at the Potchefstroom University for Christian Higher Education and was awarded a B.Sc. degree in 1944 majoring in Botany and

Chemistry. In 1945 the Potchefstroom Teachers College awarded him the Transvaal Teachers' Diploma and from 1946 to 1950 he intermittently furthered his teaching career while continuing with postgraduate studies.

In 1949 the Potchefstroom University for CHE conferred a M.Sc. degree in Botany on him and from June 1951 to March 1955 he was employed as plant ecologist in the Kruger National Park, during which time he undertook an ecological survey of the vegetation of the Park. He also established the well-known herbarium at Skukuza. During this time he collected more than 4 300 herbarium specimens, many of which were recorded for the first time in South Africa, as well as several new species. During the period of his employment in the Park he also established experimental burning plots in the major habitat types that are still monitored today and furthermore, laid the foundation for the burning policy of the Park.

In 1958 he received a D.Sc. degree (cum laude) in Botany from the Potchefstroom University for CHE presenting a thesis entitled: '*n Ekologiese studie van die flora van die Nasionale Krugerwildtuin* (An ecological study of the flora of the Kruger National Park). This work served until recently as the foundation for many ecological studies in the Kruger National Park.





FIGURE 3.—Hermanus Phillipus van der Schijff (1921–1977).

Upon leaving the Parks Board he accepted a post as professional officer in pasture science in the Agricultural Faculty of the University of Pretoria, in March 1955. Subsequently, in 1956 he became a lecturer, and later senior lecturer in Botany at the same University where in 1964 he was appointed Head of the Department of General Botany and occupied the Louis Botha Chair.

Through his enthusiasm and dedication, plant ecology was established as a major discipline in the department and this later developed into one of the recognised ecology groups in South Africa. The success of his teaching career is reflected in the many students who have obtained their postgraduate qualifications under his supervision and guidance and who still today occupy important positions in botany.

In 1972 Prof. van der Schijff became Dean of the Faculty of Natural Sciences and in 1973 a member of the University Board. From 1982 until his retirement on 31 December 1986 he was Vice-Principal of Natural Sciences at the University of Pretoria. Prof. van der Schijff made many significant and lasting contributions in his capacity as Dean, Vice-Principal, member of the University Council and the Executive Committee of the Senate, as well as member and vice-chairman/chairman of many other committees, bureaux and councils at the University of Pretoria.

Throughout his university career Prof. van der Schijff remained active in collecting herbarium material, in total more than 8 000 numbers, mostly at Mariepskop (Figure 4), in the Northern Province (northern Transvaal) and in Namaqualand.

During 1965, with the support of the CSIR, he did post-doctoral research as a 'Mercer Research Fellow' at the Arnold Arboretum, Harvard University. En route there and back he visited various botanical institutes in England, France, The Netherlands, Germany, Austria and Switzerland. He also visited Puerto Rico in the Caribbean Sea. During 1969 he again visited several universities abroad, and in the United States of America he investigated the teaching methods of biology followed at American schools and the transition between school and university. During this visit he also attended the International Botanical Congress in Seattle where he delivered a paper. On invitation he also attended the centenary celebrations of the Arnold Arboretum. On his return to South Africa he again visited several universities in France, Germany, Switzerland and Austria. In 1974 he attended the VIIIth AETFAT Congress in Geneva, Switzerland.



FIGURE 4.—Prof. Manie sitting on *Encephalartos* sp. during one of his field trips.



During 1980 Prof. van der Schijff, with financial support from the CSIR, visited universities and botanical institutes in the United States of America and Europe including a visit to the house of Linnaeus in Uppsala, Sweden. After this he attended a symposium in Nice, France during 1981 as a guest of Sperry-Univac, at the same time also visiting several computer companies in Paris. In 1985 he again attended the AETFAT Congress, this time in St Louis in the USA.

Included in his extracurricular activities were, inter alia, full membership of the 'Suid Afrikaanse Akademie vir Wetenskap en Kuns' (South African Academy of Sciences and Art), Vice-chairman of the Academy Council and Chairman of the Council of the Faculty of Natural Sciences and Technology. Furthermore he was also a member of the editorial board of the *Tydskrif vir Natuurwetenskap* (Journal of Natural Sciences).

Prof. van der Schijff was also a member of several professional scientific societies. He was President of the Joint Council for Natural Scientific Societies (1970–1971), The South African Association of Botanists (1971–1972), and The South African Biological Society (1971). He was Vice-chairman of the Transvaal Museum Board, Member of the Executive Committee of The Transvaal Board for Nature Conservation, Honorary President of The South African Aloe and Succulent Society, Member of the Botanical Advisory Committee of the Department of Agricultural and Technical Services, and finally, a board member of the Associated Scientific Societies of South Africa. Other noteworthy appointments include membership of the senate of the University of Transkei, Rand Afrikaans University, University of Venda and the University of Durban Westville; and of the Faculty Board for Natural Sciences of the University of South Africa.

It must be recorded that Prof. van der Schijff played a major role in the establishment of the Joint Council for Natural Sciences and the South African Association of Botanists.

The youth of South Africa were always very important to Prof. van der Schijff and it is little wonder that he was deeply involved in the field of education. As a member of the Joint Matriculation Board he was Chairman of the Committee for Biological Sciences and a member of the Biology Curriculum Committee while also serving on the Examination Board of the Department of Education and Development. In addition he was a member of the Board of Moderators of the Transvaal Department of Education, moderator for Biology and Botany of the Joint Matriculation Board and for Biology for the Transvaal Department of Education. During the period 1979/1980 he served as Chairman of the Joint Matriculation Board and was nominated to serve on the Supervisory Committees for experiments with the curricula and curriculum development in the Transvaal and Cape Province.

Prof. van der Schijff was jointly responsible for the establishment of the postgraduate course in Wildlife Management at the University of Pretoria. Twenty-seven masters and sixteen doctoral students graduated under his supervision.

As academic and researcher, Prof. van der Schijff was author and co-author of over eighty research papers, textbooks in general botany and manuals for practical courses in botany at university level. He was also co-author and planner of several textbooks in biology for secondary schools.

Prof. van der Schijff is not only known in the academic world but through his contributions in the Afrikaans newspaper 'Die Beeld' and many appearances on radio and television programmes on environment and environmental management issues—he became a familiar name in many households. He also delivered many popular talks on nature and environmental conservation issues.

Until his death he was intimately involved with the environmental management of Krygkor terrains and the Lesotho Highland Water Project.

He received many awards for his immense contribution to science and biology at school and university level, more specifically the environmental sciences. The awards included the Senior Captain Scott Medal from the South African Biological Society, the Havenga Prize for Biology from the South African Academy for Sciences and Art, Honorary Doctorates from the Potchefstroom University for CHE and the University of Pretoria, Medal and Honorary Award from the South Africa Federation of Science and Mathematical Teachers, Medal from the Joint Matriculation Board, The Silver Medal of the Order of Meritorious Service from the State President and the Medal of Merit for Environmental Management from the Krygkor Group. The gardens surrounding the buildings of the Botany Department at the University of Pretoria are named after Prof. van der Schijff (Figure 5).



FIGURE 5.—Prof. Manie admiring a *Sireltzia* in the University garden which is named after him.

In his youth Prof. van der Schijff was active in sport and he was captain of the first rugby team of the Ventersdorp Secondary School and of the first rugby team and rugby club of the Potchefstroom Teachers' College. He also played for Western Transvaal. Furthermore, he was the under-19 rugby coach for the University of Pretoria and a selector for Northern Transvaal.

At the University, Prof. van der Schijff was well loved by his students. Although he was very strict, he was reasonable in his expectations and always had something humorous to share with his students. His involvement with student rugby and student activities, such as being President of the Student Biological Society, the Student Science Society and the Cross Country Society, was appreciated by the students. In 1986 the Students Council of the University of Pretoria honoured Prof. van der Schijff with the Dux Docens Award.

Prof. Manie was married to Miss Joy van Niekerk of Senekal in the Free State and they have three sons and three daughters all of whom have good university qualifications. The Van der Schijffs were always a closely knit family, and as one of his sons put it, there was never a dull moment in their home when Prof. Manie was around. As a student of Prof. van der Schijff, I personally can only agree with him.

The above account bears ample evidence of the great role this beloved professor played in the development of botany and science in South Africa.

#### ACKNOWLEDGEMENTS

Mrs Joy van der Schijff and Mr Herman van der Schijff, one of his sons, supplied much of the information for this tribute to Prof. van der Schijff.

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### MICHIEL (MIKE) ADRIAAN NIKLAAS MÜLLER (1948–1997)

Michiel (Mike) Adriaan Niklaas Müller (Figure 6), second curator of the National Herbarium of Namibia (South West African Herbarium) died tragically in a motor car accident on 4 April 1997. Botany in Namibia has lost a valued scientist and colleague in the prime of his career at age 49.

Mike, as he was affectionately known, was born in Citrusdal in the Western Cape, South Africa, on 25

January 1948, where he also matriculated before registering for a B.Sc degree at the University of Stellenbosch. After graduating in 1970, he took up the position of Professional Officer at the SWA Herbarium in Windhoek. In 1973 Mike took leave of absence for a year to obtain his B.Sc. (honours) degree at the University of Pretoria.

By the time he succeeded Mr Willy Giess as Curator in 1975, Mike had already developed a keen interest in the genus *Eriocephalus* (Asteraceae), which also formed the subject of his Masters degree from the University of Pretoria obtained in the same year. An extensive taxonomic revision of the genera *Lasiospermum* (Asteraceae) and *Eriocephalus*, resulting in the description of four new species of the latter (unpublished), earned him a Ph.D. from the University of Stellenbosch in 1988. (Efforts are currently under way to have his thesis published, hopefully in *Bothalia*). Mike held the position of Officer-in-Charge of the Herbarium and Agricultural Laboratory until his promotion to that of Deputy-Director of Forestry in 1991.

Mike's infectious enthusiasm for the unique Namibian flora and his incomparable knowledge thereof, resulted in numerous popular articles. His impressive and informative exhibits of indigenous plants at the annual Agricultural Show in Windhoek contributed largely to public awareness of our flora (Figure 7). Mike is perhaps best known for his publication *Grasses of South West Africa/Namibia*, available in three languages (Müller 1984). This book, covering over 115 grass species, the majority of agricultural importance and each accurately illustrated in black and white by the artist Blythe Loutit, continues to be in great demand by scientists, students, farmers and tourists. At the time of his tragic death, Mike was completing a monumental work on the *Trees and shrubs of Namibia*, a project which had kept him occupied for almost 15 years. It is anticipated that the book will be published in the foreseeable future. We have no doubt that it will be hailed as a historic and comprehensive reference work.



FIGURE 6.—Mike Müller with artist Christine Marais, at the Namibia exhibit for *Flora '88*.



FIGURE 7.—Mike in lily pans (*Crinum paludosum*) near Maltahöhe, Namibia.

Mike collected widely in Namibia (Figure 8). His collections are housed both in the National Herbarium of Namibia (WIND) with  $\pm 1\ 070$  numbers and the National Herbarium, Pretoria (PRE) totalling 580 numbers (57 with Willy Giess).

Mike is survived by his wife Petro (née Scholtz), a lecturer in Afrikaans at the Windhoek College of Education, and by three daughters and a son.

For those of us who had the privilege of working closely with Mike, his death is far more than the passing of a colleague. He was a sincere and generous person who cared about others and displayed all those characteristics which we associate with inherent goodness but which are, alas, so seldom encountered. His influence will continue to be felt through his writings and the love of plants he instilled in the hearts of so many.

#### ACKNOWLEDGEMENTS

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GILLIAN MAGGS\* AND G. GERMISHUIZEN\*\*

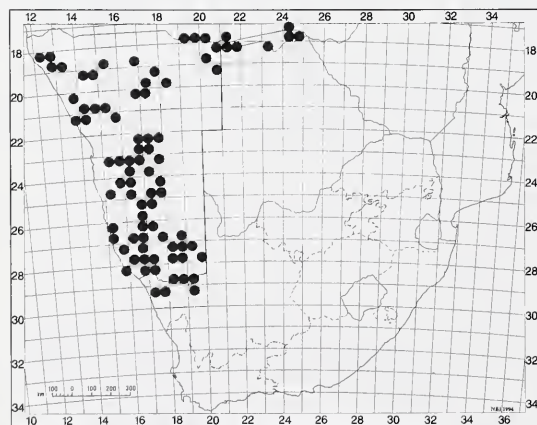


FIGURE 8.—Grids where Mike Müller collected.

\* National Herbarium of Namibia, Private Bag 13184, Windhoek, Namibia.

\*\* National Botanical Institute, Private Bag X101, 0001 Pretoria.

## Book Reviews

VEGETATION OF SOUTHERN AFRICA, edited by R.M. COWLING, D.M. RICHARDSON & S.M. PIERCE. 1997. Cambridge University Press, The Edinburgh Building, Shaftsbury Rd, Cambridge CB2 2RU, UK. Pp. xxxiv + 615. Hard cover: ISBN 0-521-57142-1, price £125.00, \$225.00.

It has been said that southern Africa contains all the world's vegetation types in one country and even, as is stated in the book, 'the world in one country'. For the uninitiated this may seem to be a gross exaggeration but as one experiences the variety of biological and social life, the appeal of the diverse landscapes and the vagaries of the climate in different areas, the truth in this statement becomes apparent. The challenge to South Africa's botanists has been how to document and do justice to the outstanding diversity of southern Africa's vegetation in a single volume. To answer this challenge, the collective expertise of the research fraternity currently concerned with vegetation-related studies on the African subcontinent was drawn together. By involving experts to write on particular aspects of the vegetation in southern Africa and related topics, under the guidance of excellent editorship, it has been possible to compile the most comprehensive compendium of information on southern Africa's vegetation to date.

Apart from its remarkable floral diversity South Africa has also been endowed with remarkably dedicated scientists in the fields of plant ecology and vegetation science. This publication is dedicated to one of these, John Acocks, whose seminal work *Veld types of South Africa* formed the basis and inspiration for much of what has followed and moreover, has been the benchmark of vegetation classification in southern Africa for many years. Liberal reference is made to Acocks's work in literature pertaining to South Africa's veld and flora and it is a fitting tribute that a book on this subject and of this quality should be dedicated to his memory.

The book is well introduced with a complimentary foreword but more importantly with a concise and informative general preface. The general preface gives the reader a good idea of the aims, scope and setting of the book and encourages one to read on in the realisation that there is still much to learn. The preface clearly introduces the structure of the book which is divided into three parts, forming a logical progression from one part to the next. Part I comprises four chapters on landscape evolution, climate, biogeography and vegetation palaeohistory which 'set the scene' and provide the reader with a framework for appreciating present vegetation patterns and processes. The second and principal part of the book consists of 10 chapters which describe the major vegetation units found in southern Africa. The treatment follows the classification of the vegetation into seven biomes and three units at the non-biome-scale. Part 3 of the book includes eight chapters on cross-biome topics such as conservation, fire, alien plant invasions and so on. The editors considered these topics to be of global interest and this approach positions the book well to capture the interest of a global audience rather than restricting its appeal to local enthusiasts.

The logical presentation of material in *Vegetation of southern Africa* makes for a relatively simple evaluation procedure. Each part of the book is separately prefaced giving a summary and breakdown of the section and the type of information one finds. The chapter material is detailed, well referenced and packed with information.

The palaeohistory of southern Africa is fascinating and the two chapters dealing with the evolution of landscapes and vegetation history transport one back in time to the 'Jurassic Park' that southern Africa once was as the land was moulded and the dynasties of different floras rose and fell. These chapters encourage one to look with new eyes at the complex landscapes that make up southern Africa and indeed to consider the 'unseen' floras which lie buried from our view. The chapter by R.E. Schulze deals with climate in a more contemporary sense and its link to the present flora of the country. It contains valuable information but it is a great disappointment that the climate maps are published in monochrome! Publication of these maps in colour (which I have seen) would have greatly enhanced the chapter since maps such as Figure 2.6 (and others) show little definition between the three darkest units—the colour hues are too close!

The overarching chapter presented on the phytogeography of southern Africa is an essential prerequisite to the contents of the following chapters. It gives the reader a clear perspective of the floral diversity of the African subcontinent by broadly analysing the phytogeography in terms of ecological, historical and phylogenetic factors, while focusing more specifically on patterns and correlates of species-level endemism. The analysis of the 'age' of different endemic species following Cronk's scheme, however superficial, is to my knowledge the first time this classification has been applied to southern African endemic taxa. This greatly assists in providing an evolutionary time-frame for the extant subcontinental flora.

Part 2 of the book commences with a chapter categorising the biomes of the African subcontinent. It could be argued that this chapter should have been included in the introductory Part I. Nevertheless it serves the purpose well of providing a foundation for the descriptive chapters on the various biomes and non-biome-scale units recognised. The period of collaboration amongst terrestrial ecologists from the mid-1970s to the late 1980s, under the umbrella of the National Programme for Ecosystem Research of the Council for Scientific and Industrial Research (CSIR), was perhaps the most important thrust there has yet been in understanding the patterns and processes in the different biomes. The immense amount of knowledge gained during this period is highlighted in the chapters presented here and the specific intention of achieving some uniformity of treatment of the different biomes is useful for comparative purposes. The approach has, however, also been adequately flexible to allow for the special aspects of each biome to be exposed, e.g. the lichen fields of the desert or the intriguing reproductive biology of some plants in the fynbos and succulent karoo. The approach has thus been thorough and comprehensive and the valuable aspect of all the chapters in this section has been the identification of gaps in existing knowledge. There are numerous recommendations for future research to answer pressing questions; some of the questions are of 'academic interest' but most have a strong link to conservation. One gains a sense of urgency that these questions need answering soon to foster sustainable utilisation of southern Africa's vegetation resources from the grasslands of the interior to the kelp beds on the continental shelf and from the desert to the alpine ecosystems of the high mountains.

In the third part of the book a series of eight chapters are presented dealing with topical ecological themes. They range from the theory of species diversity to the impacts of abiotic factors such as fire and the impacts of human utilisation and alien biota on the natural vegetation. The introductory preamble to the section once again gives a helpful summary of the contents and the chapters, although entities on their own, highlight many intriguing facets which may be seen as being linked in the colourful fabric of vegetation on southern African landscapes. It is appropriate that the book should end with a chapter on conservation and South Africa can be justifiably proud of work accomplished in this arena. However, as we draw closer to the end of the millennium we need to take stock of the natural resources in southern Africa. *Vegetation of southern Africa* is well timed as it provides a good critique of the state of affairs and will serve as a valuable benchmark publication for future work.

In conclusion some further general points require mention. The layout of the book in three sections is laudable and assists the reader in the use of the book. The volume is well indexed and the short glossary is also useful, particularly for readers not familiar with many colloquial southern African terms. There are nevertheless some disappointing aspects. In a book on the vegetation of such a colourful country in terms of vegetation, landscapes and individual plant species, it is regrettable that there are no colour reproductions of photographs (and maps—see above). It is clear that many of the black-and-white reproductions were produced from colour diapositives. Although this is obviously not a 'coffee table book' I am convinced that some colour would have greatly enhanced its appeal and value; for instance the impact of Figure 22.8 is completely lost due to the lack of colour. There is also a good deal of inconsistency in the layout of captions and the fonts used for these. In some instances the captions are crammed into



single columns whereas in others they are liberally spread across the width of the page. A bold font for captions is also not appropriate. These unfortunate editorial points do detract from an otherwise outstanding publication. Lastly, the price tag on the book makes it beyond the reach of the average student, biologist and indeed many libraries such as in schools. This is also unfortunate since it will work against the popularisation of vegetation science in South Africa where literature on this subject should be much more freely accessible.

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PLANT COLLECTORS IN MADAGASCAR AND THE COMORO ISLANDS by LAURENCE J. DORR. 1997. *Royal Botanic Gardens*, Kew, Richmond, Surrey TW9 3AE, UK. Hard cover: ISBN 1-900347-18-0, price £66.70.

We have all heard of the paperless future and how computer software will in some form or another take over the function of books in the near future and so books as we know them will become obsolete, etc. This urban legend has been around for almost thirty years to my knowledge, but only in the last few weeks has it started to change from wishful thinking into something resembling reality. Laurence Dorr's splendid new book is the first I have seen that includes a CD-ROM (available separately at £27.60 outside UK or £31.80 incl. VAT in UK) that contains all the text and pictures and is searchable. The software supplied is a read-only version of Adobe Acrobat that is said (Adobe Systems 1997) to work equally well under Windows, Macintosh and Unix. Certainly it works beautifully under Windows, allowing me in short order to find each collector who had some connection with South Africa as well as Madagascar. It was most impressive, but not quite the thing for bedside reading. And this is a reference book I could well imagine wanting to read in bed.

Welcome to the brother of *Botanical exploration of southern Africa* (Gunn & Codd 1981)! Those of us who are used to the format of the local volume will find few surprises in that department, but a wealth of information, some of it new (to me at least) on collectors who worked in both Madagascar and the African mainland. Of those there are surprisingly many. The biographies are very short and to the point, but not so short as to become as dry as those in Desmond (1994). On the other hand, there is a problem with printing some of the most entertaining stories of our fellow botanists; the best stories are often not exactly flattering to their subjects. There are about 1200 collectors in this book, and some 250 of the entries include a portrait. Important publications by the collector are mentioned, as are references to other biographies, portraits, places collected and herbaria where the collections are housed. Only genera and some non-botanical items (not species) named after the collectors are noted. An interesting feature is that partnerships of two or more collectors are accorded a separate entry.

The CD in the back is an intriguing idea, and raises the question: shouldn't we be thinking of borrowing the idea for the presentation of our floras? Just imagine if one had the whole published *Flora of southern Africa*, including corrections and contributions published in *Bothalia* all on one CD. Even a fairly simple search routine would be usable for a rough-and-ready key. And if relatively few copies were produced in a run, the CD-flora could be updated quite often.

In conclusion, I am delighted to have my own copy of this book, and would recommend that any organisation involved in botanical research on Madagascar, the Comores or the east coast of Africa, should have a copy.

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H.F. GLEN\*

FIELD GUIDE TO TREES OF SOUTHERN AFRICA by BRAAM VAN WYK & PIET VAN WYK. 1997. *Struik Publishers*, 80 McKenzie Street, 8001 Cape Town. Soft cover: ISBN 186825-922-6, price R149.00.

The simplest and most effective way of describing something new is to compare it with something known. Just think of the diagnostic names and descriptions of Father Linnaeus or the common names given by immigrants from Europe to plants and animals in this part of the globe. How better then to introduce the dendrofriend to the new book by two of the botanical Van Wyks than to compare it with the well-known work by Elsa Pooley (1993).

In many ways the two books are very similar. They cost between R120.00 and R150.00, they measure 210 × 150 × 30 mm and weigh about 1 kg, more or less the size and weight one has become familiar with in field guides to birds, beasts, trees and flowers in many parts of the world. Van Wyk & Van Wyk, in 536 pages, describes and illustrates about 815 tree species, with further notes enabling the reader to identify more than 1 000 native and naturalised species found in Africa south of the Cunene, Okavango and Zambesi Rivers. Pooley deals with 780 species found in KwaZulu-Natal and Transkei (Eastern Cape) in 572 pages.

In the Van Wyk book the trees are classified into 43 groups based on easy-to-observe vegetative characters. Each group is assigned an icon which summarises some of the group's diagnostic features. A dichotomous key based entirely on vegetative characters, enables the reader to establish the group to which a specimen belongs. The groups are arranged in six major groupings, such as *leaves simple and opposite*, indicated by colour coding also displayed in the form of thumb indices. Each group starts with a concise statement of its diagnostic characters. The trees within each group are arranged alphabetically according to family and within the family alphabetically according to scientific name. A distribution map is given for each species dealt with in detail. The colour of the shading on the maps, giving the approximate outline of the distribution area of the species in the region, indicates whether a species is endemic, or native to the region and also found further north, or a naturalised alien. At least one, but usually two colour photos are given for each species. Two to five, but usually three or four, species are dealt with on two facing pages. Each species entry starts with the scientific name (without author name), recent synonyms, vernacular names in English and Afrikaans and the tree number according to the National Tree List (Von Breitenbach 1989, 1995) and/or the Zimbabwe Tree List (Drummond 1981) as well as the flowering season. In the descriptions of about 60 to 70 words, diagnostic characters are printed in bold. A brief paragraph on the uses of the tree is often added. Related species not figured or mapped are sometimes briefly described.

The Introduction discusses the geographical area covered and some of its features. A map shows its biomes and vegetation types and another the centres of plant diversity and endemism. Brief chapters advise the reader on how to identify trees, how to use the book, and another provides a guide to the species accounts. The key to the 43 groups occupies three pages. Descriptions of about 100 families mention the common name, outstanding features and the representation in the area. The book ends with a glossary of terms illustrated by line drawings and photos, selected references and contact addresses, acknowledgements and an index. The inner back cover provides a quick guide to the 43 groups as well as a ruler marked in cm and mm.

The main difference between the Van Wyk and the Pooley book, apart from the much smaller area covered by the latter, is the way in which species can be identified. Pooley provides a key, also based largely on vegetative characters, which leads directly to the species with accompanying photos and map. The key in Van Wyk may leave you with a choice of more than a hundred species which must be made mainly with the aid of maps and illustrations. The key in Pooley is obviously much longer and much more challenging and compels the reader to have a much closer look at the tree to be identified. The species descriptions in Pooley are more detailed giving information on bark and stem and many measurements but highlighting fewer diagnostic features. The KwaZulu-Natal book provides the names of authors of scientific names and, in addition to English and Afrikaans names, many names from Zulu and Xhosa. An important feature given in Pooley but not in Van Wyk are small leaf sketches of all species placed between the distribution maps, an area left blank in Van Wyk. This adds to the impression one gets with the work by the Van Wyks that space is underutilised.

The Preface of Van Wyk states that the book contains the most comprehensive collection of photographs of trees ever published in south-

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ern Africa. Piet van Wyk, we are told, covered some 160 000 km since 1992 to amass a collection of more than 30 000 colour photographs. One look at the photos shows that Piet is a highly experienced photographer and that he had a vast selection of material to choose from. The photos in Pooley are generally not of the same standard but usually not much less informative; and there is something to be said for the largely natural backgrounds in the Pooley close-ups in contrast to the bible-black studio-type backgrounds of Van Wyk. The standard of colour printing of the KwaZulu-Natal book is also markedly lower, as can be seen when comparing the same photo of *Pterocelastrus echinatus* reproduced on p. 171 in Van Wyk and on p. 275 in Pooley. Van Wyk is only available in soft cover. Pooley can also be had in hard cover which I find definitely preferable. The binding of the Van Wyk work appears to be sound and much less likely to disintegrate like that of at least the first edition of the *Field guide to the wild flowers of the Witwatersrand & Pretoria region* by Braam van Wyk & Sasa Malan (1988). The final editing and proofreading of the Van Wyk work is excellent; the few blemishes noticed do not warrant mention. It could be asked, however, why *Securidaca longepedunculata* is spelled differently from the original correct spelling?

Which of the two works is the better buy? Anybody living outside KwaZulu-Natal will probably choose Van Wyk, if only for its much wider geographical coverage. Residents of the province on the eastern seaboard with an intense interest in their trees will most likely go for

Pooley. For those who hesitate, the choice is clear: buy them both. They are both excellent value for money.

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## Errata in *Bothalia* 27,2 (1997)

COETZEE, J.C., EICKER, A. & VAN WYK, A.E. Taxonomic notes on the Geastraceae, Tulostomataceae, Nidulariaceae and Sphaerobolaceae (Gasteromycetes) *sensu* Bottomley, in southern Africa: 117–123.

p. 121:

2.2.2 Batarrea Diqueti *Patouillard et Hariot* (621)

The transfer of this fungus to the genus *Battarreoides* Herrera (Heim & Herrera 1961) has been widely accepted (Dring 1973; Hawksworth *et al.* 1983; Miller & Miller 1988; Coetzee & Eicker 1994; Moreno *et al.* 1995). The correct name and author citation is **Battarreoides diquetii** (*Pat. & Har.*) *R.Heim & T.Herrera*.

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p. 122:

COETZEE, J.C. & EICKER, A. 1994. *Battarreoides diquetii* (Gasteromycetes, Tulostomatales) in southern Africa. *Mycotaxon* 50: 19–25.

should read:

COETZEE, J.C. & EICKER, A. 1994. *Battarreoides diguetii* (Gasteromycetes, Tulostomatales) in southern Africa. *Mycotaxon* 50: 19–25.



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